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Historical Biogeography and Natural History of Nocturnal Wasps in the Southwestern Deserts with Special Emphasis on the Genus Chyphotes (Hymenoptera: Chyphotidae)

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HISTORICAL BIOGEOGRAPHY AND NATURAL HISTORY OF NOCTURNAL WASPS IN THE SOUTHWESTERN DESERTS WITH SPECIAL EMPHASIS ON THE GENUS *CHYPHOTES* (HYMENOPTERA: CHYPHOTIDAE)

by

Emily A. Sadler

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ABSTRACT

Historical Biogeography and Natural History of Nocturnal Wasps in the Southwestern Deserts with Special Emphasis on the Genus *Chyphotes* (Hymenoptera: Chyphotidae)

by

Emily A. Sadler, Doctor of Philosophy

Utah State University, 2018

Major Professor: Dr. Joseph S. Wilson
Department: Biology

Evolutionary biologists and biogeographers are exceedingly interested in desert regions, which at first glance are seemingly depauperate, but actually rank among the most species rich of the biomes. Nocturnal wasps (Hymenoptera) are extremely abundant in deserts, but neither their taxonomy, nor their evolutionary or natural histories are well known. One light trap can yield thousands of individuals in a matter of hours, in particular those of the families Chyphotidae, Tiphiidae (Brachycistidinae), and Mutillidae. In this dissertation, I corrected the taxonomy of one particular group of wasps that are abundantly collected, those of the black-headed *Chyphotes—C. aenigmus* Mickel, *C. atriceps* Mickel, *C. calexicensis* Bradley, *C. incredulus* Mickel, and *C. melaniceps* (Blake)—using both morphological and molecular data, and describe a new related species *C. ciaran* Sadler and Pitts, **sp. nov.** I expanded our knowledge on the distribution of the species in these three families of wasps by conducting a trap-transect study in

Joshua Tree National Park collecting 22 species of Brachycistidinae based on the collection of 13,960 specimens, 11 species of *Chyphotes* based on the collection of 1,513 specimens and 35 species of Mutillidae based on 8,477 specimens. Additionally from this transect study, three new species of Mutillidae were described as *Odontophotopsis dalyi* Sadler and Pitts, **sp. nov.**, *O. odontoloxia* Sadler and Pitts, **sp. nov.**, and *Photomorphus schoenwerthi* Sadler and Pitts, **sp. nov.** Lastly, I used novel phylogenomic methods based on ultra-conserved elements to produce the first phylogenies—molecular or otherwise—of *Brachycistis* and *Chyphotes.* I compared these phylogenies to that of *Odontophotopsis,* which was derived from Sanger sequencing data. I found that for *Odontophotopsis* and *Chyphotes* Pleistocene glaciation cycles as well as older orogenic events, albeit to varying degrees, influenced diversification in western North America. *Brachycistis* only seemed to be influenced by older Neogene orogenies. Furthermore, species-level relationships for these three groups supported inundation of southern California by the Boues Sea Embayment and a hypothesized Baja Inner Peninsular Seaway.

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PUBLIC ABSTRACT

Historical Biogeography and Natural History of Nocturnal Wasps in the Southwestern Deserts with Special Emphasis on the Genus *Chyphotes* (Hymenoptera: Chyphotidae)

Emily A. Sadler

Deserts are interesting places due to the large number of plants and animals that live there. Nocturnal wasps are extremely abundant in deserts, but they are difficult to identify and their life cycles are not well known especially the families of Chyphotidae, Tiphiidae (Brachycistidinae), and Mutillidae (velvet ants). In this dissertation, I determine how to correctly identify a particularly difficult group of species that all have black heads from the family Chyphotidae. This is important because these species make up a large proportion of specimens collected. Also, I expanded our knowledge on the distribution of the species of these three families of wasps by conducting a trap-transect study in Joshua Tree National Park catching 22 species of Brachycistidinae based on the collection of 13,960 specimens, 11 species of *Chyphotes* based on the collection of 1,513 specimens and 35 species of velvet ants based on 8,477 specimens. From this study, three new species of velvet ants are described: *Odontophotopsis dalyi* Sadler and Pitts, **sp. nov.**, *O. odontoloxia* Sadler and Pitts**, sp. nov.**, and *Photomorphus schoenwerthi* Sadler and Pitts, **sp. nov.** Lastly, I used new molecular methods to determine relationships of the species of *Brachycistis, Chyphotes,* and *Odontophotopsis.* These relationships suggest

that the species are young, which is contradictory to evidence based on birds and mammals. These relationships also support dates for the inundation of southern California by the Boues Sea Embayment and confirm a hypothesized Baja Inner Peninsular Seaway.

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Emily A. Sadler

CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

North American Desert Biogeography

Earth is home to many biomes. Each biome supports life in a variety of forms and functions, and each is home to organisms specialized to tolerate their unique conditions. One biome with seemingly restrictive conditions is the desert. The word 'desert' implies a general lack of the one thing that sustains life, water. Because of this restriction deserts are often misconstrued as being nothing more than post-apocalyptic wastelands. Oddly enough this 'wasteland' occupies as much as one quarter of the earth's surface (Polis, 1991), and occur in some form on all the continents (Larson, 1977). From the polar deserts of the Arctic to the hottest deserts of the Sahara, the globe is dominated by these ostensible unproductive landscapes. Despite a superficial display of sterility, most deserts are rich in species-level diversity of plants and animals.

Before delving into the specifics of desert research past and present, a definition of a desert should be explicitly made. As is typical in scientific research, a consensus on the true definition of a desert is debatable. Some authors say regions with less than 15 inches of annual precipitation should be designated as semi-arid deserts, and deserts (in the truest form) only occur when less than 5 inches of annual precipitation are received (Shmida, 1985; Cloudsley-Thompson, 1965). Most authors define a desert as having less than 10 inches of precipitation per year (Cloudsley-Thompson, 1965; Larson, 1977; Jaegar, 1957), and that is the definition I will use. In addition to having limited precipitation, deserts also exhibit extreme temperatures and continuous erratic winds; all

three of these factors exacerbate already low moisture levels. Soil type or substrate varies in deserts as well, with only 20 percent being sand (Seely, 1991). Of particular importance from an anthropocentric perspective, as these are the deserts we live near in North America, are the sub-tropical deserts (Mojave, Sonoran, and Chihuahuan) and the cold deserts (the Great Basin and Colorado Plateau). Approximately 6,000,000 square miles of the earth is covered by these deserts (Larson, 1977).

Of all the deserts in the world, those of particular importance to my research are the subtropical and cold deserts of the United States. Although encompassing 500,000 square miles, the deserts of North America are only the 5th largest expanses of desert landscape in the world, preceded only by the Sahara in Africa, the Australian Deserts, the Arabian Desert, and Turkestan in Russia (Larson, 1977). Examples of extremes in these deserts are: an average of only 1.2 inches of rainfall over a 14 year timespan in the Sonoran deserts (Larson, 1977), temperatures maxing at 134˚F in Death Valley (Jaegar, 1957), and swells of wind called “chubascos” reaching 80-100 miles per hour (Larson, 1977; Jaegar, 1957). Although the Southwest does not get as frequent a rainfall as other areas, and moisture is remarkably low, sand itself allows for greater retention of the water it does encounter (Fet, 1998). The ability to retain water, even during times of drought, contributes to the success of communities establishing themselves in these extreme niches. With relatively no humidity and a ‘feast-famine’ fluctuation of rainfall (MacMahon, 1979), the Southwestern portion of the United States is home to spectacularly well-adapted flora and fauna.

There are two major causes of desert formation. One cause of subtropical desert formation is due to air circulation around the desert belts that fall around 30˚ north and 30˚ south of the equator (Cloudsley-Thompson, 1965), also known as Hadley cells. Warm air in these regions cycle from high altitudes towards low altitudes; as the cold air moves down in elevation, it warms quickly and dries as it moves towards the surface of the Earth. The dry air is now incapable of precipitation resulting in the arid climates of the subtropical deserts (Brown, 1968). This can explain what causes the formation of the four largest subtropical deserts in the world (Sahara, Australian, Arabian, and Turkestan), but only accounts for a portion of the desert formation in North America. Subtropical deserts of North America are limited to the Northern part of Mexico, and the very Southern portions of the United States (Brown, 1968). Only part of the Sonoran and Chihuahuan deserts can be described in this manner.

A second major cause of desertification is rain shadows caused by local mountain ranges. This accounts for the majority of the United States deserts. The Mojave, Great Basin Desert, and Colorado Plateau being a result of the Sierra Nevada and Rocky Mountain ranges, the Sonoran Desert a result of Peninsular and Sierra Madre Occidental ranges, and the Chihuahuan Desert from Sierra Madre Oriental and Sierra Madre Occidental ranges (Shmida, 1985; Thorne, 1986; Larson, 1977; Wilson and Pitts, 2010a). Although the formation of the Southwestern deserts are agreed to be a result of mountain orogeny and the subsequent rain-shadows they cast, the dates attributed to events of uplift and desertification are highly variable (Wilson and Pitts, 2010a). Interpretations from different perspectives (i.e. geological versus paleobotanical), and interpretations written

during different times of development in the field of geoscience under different levels of understanding in global tectonics, lead to such discrepancies. Geological dating is not absolute and, therefore, the dates ascribed by using such methods should be used more as a generality than an absolute time period (Wilson and Pitts, 2010a).

The diversification of the North American desert biota can be linked to geological events that lead to the formation of the desert, although the timing of the specific events have been debated, a consistent pattern is beginning to emerge. Late Neogene uplift seems to be playing a central role in diversification of organisms in these arid climates (Riddle and Hafner, 2006). For instance, genetic divergences now are being linked to postulated late Neogene vicariant events (Pitts *et al.*, 2010b). Two events are often credited for driving diversification in desert-adapted taxa in the North American warm deserts. Uplift of the Sierra Madre Occidental, Rocky Mountains, and Colorado Plateau during the Neogene is considered to have fragmented an ancestral arid region leading to genetic divergences between Chihuahuan Desert populations and Sonoran Desert populations, subsequently causing speciation. Second, extension of the Sea of Cortez, called the Boues Embayment, during the late Neogene likely isolated populations in the western Sonoran and Mojave deserts from populations in the eastern Sonoran Desert, leading to speciation (Pitts *et al*. 2010b; Wilson and Pitts 2010b). Phylogeographic analyses of several vertebrate taxa have revealed genetic splits that have been linked to these Neogene vicariant events (Morafka, 1977; Jaeger *et al.*, 2005; Devitt, 2006; Douglas *et al.*, 2006). Although the cold desert regions (Great Basin Desert and Colorado Plateau) have not received as much attention as the regional warm deserts, some studies

suggest that the cold desert biota may also show consistent historical biogeographic patterns, with Great Basin populations being genetically distinct from neighboring Colorado Plateau populations (Epps *et al.*, 1998; Orange *et al.*, 1999; Wilson and Pitts 2012). Additionally, the dates determined by geological and biological methods for each of the major geological events are conflicting or have enormous ranges (Wilson and Pitts, 2010a).

The majority of investigations into the historical biogeography of the North American deserts have been accomplished using vertebrate taxa (e.g., Riddle, 1995; Orange *et al.*, 1999; Riddle *et al.*, 2000a; Riddle *et al.*, 2000b; Zink *et al.*, 2001; Jaeger *et al.*, 2005; Devitt, 2006; Douglas *et al.*, 2006; Riddle and Hafner, 2006). Work conducted on vertebrate taxa often result in conflicting views of the causes of diversification. As previously mentioned, whether older or more recent geological events are more important to diversification is often debated. Pocket and grasshopper mice have been studied by Riddle (1995) to understand the divergence of aridland rodents along the North American Cordillera. His research suggests that glacial cycles in the Pleistocene had less of an influence on rodent divergence than late Tertiary to early Quaternary events (Riddle 1995). In contrast, Arbogast *et al.* (2001) studied tree squirrels and determined that late Pleistocene events where the influencing factor in diversification for his organism. Different species occurring in the same regions seem to indicate different causes for diversification. Without a more widespread examination of multiple taxa in the same regions a clear idea of the true causes for diversification cannot be agreed upon. Although some phylogeographic analyses have been performed with invertebrate taxa, particularly

arthropods, most of these have focused on local patterns like a single desert or a transition zone between deserts rather than a region-wide analysis (Epps *et al.*, 1998; Smith and Farrell, 2005; Crews and Hedin, 2006). For instance, Ayoub and Riechert (2004) investigated phylogeographic patterns in a widespread desert-adapted spider, but, because the diversification of this species was linked to Pleistocene climatic cycles, the patterns of divergence cannot be compared with the earlier Neogene diversification events found in the vertebrate taxa. Little work on region-wide patterns, however, has been conducted using arthropods.

Before a generalized model of historical biogeography in the Nearctic deserts can be developed, investigations into the diversification of arid-adapted arthropods must be conducted and compared to analyses detailing the causes of diversification in vertebrates. Likely arthropod candidates to investigate the biogeographic history of North America's deserts are species of the wasp families Chyphotidae and Tiphiidae (Hymenoptera). Biogeographical analyses of the related group of nocturnal wasps, the velvet ants (Mutillidae), have produced interesting results and are helping to better establish the timing of key geological events in the southwestern United States (Pitts *et al.*, 2010b; Wilson & Pitts, 2010b, c; Wilson *et al.*, 2010, Wilson *et al.*, 2011). Most notably, both recent Pleistocene glaciation cycles and older orogenic events, albeit to a somewhat greater extent, were both causes of major diversification in nocturnal velvet ants (Pitts *et al.*, 2010b; Wilson & Pitts, 2010b), which is contrary to current ideas produced by mammalian and avian data. Specific phylogeographic analysis have shown that both late Neogene and early Pleistocene events were influential in the diversification of

Dilophotopsis and the *Sphaeropthalma unicolor* (Cresson) species-complex, but Pleistocene climatic fluctuations seem to have been responsible for the split between the Mediterranean-adapted species and the desert-adapted species (Wilson & Pitts, 2009, 2010b, 2011). Additionally, *Sphaeropthalma arota* (Cresson) was found to be composed of four genetically distinct species that cannot be distinguished morphologically based on current methods, and is the first cryptic species-group found in Mutillidae (Wilson *et al.*, 2011). The cryptic species, however, seem to have a biogeographical pattern defined by rainfall patterns as well as aridity. Much like in the velvet ant research, we anticipate that Chyphotidae and Tiphiidae are likely to provide further insights into the evolution and geological history of the North American deserts.

Nocturnal Wasp Background

A large number of parasitoid wasps are known to be endemic to certain areas of the Southwest, in particular species in the family Chyphotidae (Mickel, 1967; Krombein, 1979) and species in the 12 genera of the tiphiid subfamily Brachycistidinae (Krombein, 1979; Kimsey and Wasbauer, 2006). Although known to occur throughout the Southwest, their abundance and richness of species in each desert has not been fully investigated or understood. Little is known concerning the life histories of Chyphotidae and Brachycistidinae, so much so that these wasps lack common names and the only publications referencing these groups are of outdated taxonomy.

Nocturnal wasps, such as Chyphotinae and Brachycistidinae, have many superficial similarities. Integumental coloration is generally brown (ranging from

yellowish-brown to black); they all have a similar body shape and size range, and share comparable patterns of distribution in the Southwest. These similarities have contributed to the difficulties in determining one family from another. Chyphotidae is segregated from other nocturnal wasps by the presence of a line of small setae on either side of the second abdominal tergum (felt line), usually a darkened patch at the tips of the forewings, and a slender petiole resulting from the elongation of the first abdominal sternum while the first abdominal tergum remains separated and only contributes to the bulbous appearance of the posterior end. Brachycistidinae are distinguished in having no felt line on their abdominal tergum, a sleek and shiny appearance (due to a lack of setae), pronounced stigma on the forewings, lamellae projecting posteromedially from mesosternum, and a more dorsoventrally flattened body.

Because these families are difficult to distinguish, most of the previous research of these groups has been devoted to the taxonomy of the males only. However, the taxonomy of both these groups still remains confused. Like velvet ants (Mutillidae), these groups exhibit extreme sexual dimorphism with males winged and females wingless. Due to this dimorphism in both Chyphotidae and Brachycistidinae, the same taxonomic problems have occurred. The number of species known only from males greatly outweighs that of those known from both sexes or only from females, suggesting that multiple species are misidentified when determining the females. For *Chyphotes*, 30 species have been described from only the male and 15 species from only the female, while only 10 species are known from both sexes (Mickel, 1967; Mickel, 1974; Krombein, 1979). For brachycistidines, there are 68 species known only from the male

and nine species known only from female, while only one species is known from both sexes (Krombein, 1979; Kimsey and Wasbauer, 2006). Additionally, the males of these groups are difficult to determine to species, because of the use of inconsistent characters in the past. The females have a completely different classification system at the generic level in Brachycistidinae. As such, taxonomic problems abound in both of these groups of nocturnal wasps, greatly hampering their use for ecological or natural history studies.

The family Chyphotidae is comprised of two subfamilies Chyphotinae and Typhoctinae (Pilgrim *et al.*, 2008). Chyphotinae has only one genus, *Chyphotes*, and two subgenera, *Chyphotes* and *Pitanta*, containing 55 species (Mickel, 1967; Mickel, 1974). Chyphotinae is only found in the Nearctic region. Most species are abundant, and the subfamily can be found from Southern Canada to Northern Mexico with the majority of species occurring in the southwestern United States. Typhoctinae is quite the opposite. Typhoctinae has four genera *Prototilla*, *Eotilla*, *Typhoctoides* and *Typhoctes*, and 10 species. These species are rarer, but this subfamily has a larger distribution. *Typhoctes* is found in the United States Southwest to Northern South America. *Eotilla*, *Prototilla*, and *Typhoctoides* are found in Southern South America in Chile and Argentina. It has been speculated that one member of Chyphotidae (*Typhoctes pecularis* Cresson) uses camel spiders (Arachnida: Solifugae) as a host (Brothers, 1995). This claim remains unsubstantiated, and due to the nature of both solpugids and Chyphotidae seems highly unlikely. Currently, the hosts of these two groups of solitary nocturnal wasps remain unknown, but are likely Scarabaeidae, Tenebrionidae, or Carabidae beetles (Coleoptera) based on evolutionary relationships (e.g., Pilgrim *et al.*, 2008). Females are solitary,

wingless, strictly nocturnal, and are well adapted to subterranean lifestyles. All of these factors make females elusive not only for collection, but also for the study of host use and other biological processes.

Tiphiidae is comprised of two subfamilies Brachycistidinae and Tiphiinae (Pilgrim *et al.* 2008). Brachycistidinae is found in the Northern hemisphere, whereas Tiphiinae is cosmopolitan (Pilgrim *et al.*, 2008). Brachycistidinae has 12 genera (*Acanthetropis*, *Brachycistellus*, *Brachycistina*, *Brachycistis*, *Brachymaya*, *Colocistis*, *Dolichetropis*, *Glyptacros, Hadrocistis, Paraquemaya*, *Sedomaya,* and *Stilbopogon*) and a total of 77 species (Kimsey and Wasbauer, 2006). Males are collected in much higher numbers, resulting in a taxonomy relying heavily on one sex. With the exception of the three largest genera (*Brachycistis*, *Stilbopogon*, and *Colocistis*), most genera are known from a single sex. Females have been placed into genera without being actually associated with any male. As is true of other nocturnal insects, females are exceptionally rare and associations are difficult. Due to the lack of specimens, and difficulty of capture, their natural history remains unknown. Six of the 12 genera known today contain only 1-2 species illustrating the difficulty of identification and the poor state of the current taxonomy.

Taxonomic Background of *Chyphotes* and Brachycistidine Tiphiids

In 1865 Cresson described a male nocturnal wasp which he placed in *Mutilla* (Mutillidae) (Buzicky, 1941; Mickel, 1967). Considering that the majority of nocturnal

wasps share a similar brown coloration, shape, and general size it is understandable that this first *Chyphotes* was misplaced. It took another 21 years before the genus *Chyphotes* was created for the female of *Chyphotes elevatus* Blake. Slowly, and in a piecemeal fashion, scientists working on this unique group realized that species had erroneously been placed in the other genera, and males began to be correctly assigned to *Chyphotes*. Once examination of the male genitalia began, the division between different species became more pronounced.

Buzicky was the first to publish a monograph on *Chyphotes*. He was also the first to associate a male and female of a single species (*Chyphotes albipes* Cresson) (Mickel, 1967). Perhaps the greatest contribution by Buzicky was his examination of the male genitalia. He was the first to extract and illustrate *Chyphotes* genitalia (Mickel 1967), and to shed light on the importance of those characters for identifications. It was realized, largely in part due to genitalic differences, that there were two distinct groups of *Chyphotes*. *Chyphotes* is comprised of two subgenera *Chyphotes* and *Pitanta* (Mickel, 1967). Division at the subgenera and species level in *Chyphotes* has been largely impacted by the use of genitalic characters. The last major revision of this genus was made in 1967 by Mickel. Mickel added 18 species (nine males and nine females), and two subspecies (both male) to *Chyphotes*, and 13 species (11 males and two females) and one subspecies (male) to *Pitanta*. Thanks to his revision, the genus now contains a total of 55 species.

It is impressive that something that has been recognized in collections since 1865 remains problematic. Despite *Chyphotes* being recognized as its own genus by 1941, the

placement at the family level of Chyphotidae has continued to be difficult. It was considered to be a subfamily of Mutillidae (Apterogyninae) until it was placed into a newly erected family Bradynobaenidae by Brothers (1975). *Chyphotes* and *Typhoctes* were considered a part of Bradynobaenidae until 2008 when Pilgrim *et al.* determined that these genera were separate from the rest of bradynobaenids and created the family Chyphotidae.

The progress that has been made over the past 150 years has led to a great advancement in the taxonomy of Chyphotidae. Despite these huge advancements, the species-level taxonomy is still in desperate need of revision, because of the large number of species known from a single sex. Most of the females have newer names that will be lost to synonymies once associations are made. Although there are at least three species that have yet to be described, the genus, which has 55 species currently, will be reduced to less than 40 species once sex associations are made.

Brachycistidinae has a similar past to Chyphotidae. These wasps are abundant in arid environments of Western North America and have, therefore, been collected alongside *Chyphotes* throughout the years. Not surprisingly they have been misplaced with *Chyphotes* in Mutillidae since the late 1800's as well. Initially both *Chyphotes* and *Brachycistis* were moved into the tribe Chyphotini within Mutillidae, but once Chyphotinae was moved to Bradynobaenidae in 1975, Brachycistidinae was also moved to the family Tiphiidae (Brothers 1975).

The species-level taxonomy of this subfamily is also confused. It has the same problems as *Chyphotes* due to the difference between the sexes. However, unlike

Chyphotes, different genera have been described for the females as compared to the males. Thus, sex associations are further behind for this group as compared to *Chyphotes*. Males were initially placed in one genus, while all the females were placed in another. The taxonomy has, therefore, been made based mainly on the males.

Chapter Objectives:

2. Use molecular data to determine species validity in a difficult group of *Chyphotes*.

3. Determine the species of velvet ants (Mutillidae) in Joshua Tree National Park.

4. Determine the species of *Chyphotes* (Chyphotidae) and Brachycistidinae (Tiphiidae) in Joshua Tree National Park.

5. Compare historical biogeographical patterns of *Brachycistis* and *Chyphotes* based on ultra-conserved element data with work already completed in velvet ants (Mutillidae).

Research

In Chapter 2 some of the most problematic taxonomic issues in Chyphotidae are discussed and resolved. Although the taxonomy of *Chyphotes* was revised by Mickel (1967), a great deal of taxonomic confusion remained in the group, particularly the *C. melaniceps* species-group, which has a distinct color pattern where the head is blackened and contrasts with the reddish-brown body. There are five species that share this color pattern, *C. aenigmus*, *C. atriceps*, *C. calexicensis*, *C. incredulus*, and *C. melaniceps*. Externally these males have no morphological differences; the division of species is

heavily based upon subtle differences in genitalic structure which some entomologists do not think justifies separation into different species. I investigated the validity of these black-headed species with a pairwise comparison of molecular data derived from the mitochondrial cytochrome c oxidase subunit I (COI). COI was the gene of choice considering its successful use for *Chyphotes* in the past, with high level or accuracy for species identifications in insects (Ames *et al.*, 2006; Ito *et al.*, 2011), and it has shown to be useful for examining intraspecific variation in Hymenoptera (Soucy and Danforth, 2002; Baer *et al.*, 2004; Kaltenpoth *et al.*, 2012). Morphological data and sequences for all five species of black-headed *Chyphotes (Chyphotes)* and for a sixth black-headed species were obtained. Also included was sequence data for five additional species in the subgenus *Chyphotes* that did not have a black-head, and five species in the subgenus *Pitanta*. The results of this analysis not only suggested these five species are, in fact, distinct species, but it also determined a sixth, new species of which I describe. Lastly, I updated the known distributions for all species.

For Chapters 3 and 4 patterns of diversity for nocturnal wasps Mutillidae, Chyphotidae, and Brachycistidinae were investigated in Joshua Tree National Park. National Parks and protected areas are important hotspots of diversity and should be studied for, at the very minimum, conservation reasons. One of the most understudied regions of the southwest is the Mojave Desert, due to the inability in the past to get permission to collect in the region. Joshua Tree National Park is an ideal area to study as its boundaries fall in both the Sonoran and Mojave deserts. This not only allows for research in the Mojave Desert, but also a transition zone between the Mojave and the

Sonoran Desert as well. Species abundance for each family was determined and then a discussion of abundance in relation to habitat, elevation, and temporal factors, such as date of collection, was conducted.

The historical biogeography of nocturnal wasps *Chyphotes*, *Brachycistis*, and *Odontophotopsis* are compared in Chapter 5. The intended use of historical biogeography is to determine relationships between geographic areas and the taxa that are endemic to them. It becomes evident that the diversity of a given region is tightly correlated with the geography of the area, which is a direct result of geological and climatic events in the history of the land. Therefore, similarities of geologic histories in these groups would suggest similar evolutionary histories (Price and Wagner, 2011). Isolation due to vicariance events should be reflected in the patterns of endemicity in these families. I completed phylogenetic analyses for each group and then examined shared patterns. These patterns indicated what events impacted these populations, and knowing roughly when these populations evolved in these areas helped elucidate time periods when these events likely occurred. My analyses help refine the dates of orogeny and desertification in the Southwest, and lessen the level of dispute; ultimately having an impact on *all* research done on organisms endemic to the Southwest. Molecular data previously amassed for *Odontophotopsis* was expanded and combined with work conducted on *Chyphotes* and *Brachycistis*. Pitts *et al.* (2010) collected molecular data over the course of 10 years from two nuclear intergenic regions (ITS1 &2) and suggested that the majority of extant nocturnal species originated between 15 Ma and 1.8 Ma in the Neogene (Pitts *et al.* 2010). In this chapter I investigate *Chyphotes* and *Brachycistis* for

similar patterns. For the latter two groups, a novel molecular approach was taken. In the past, single gene sequences were incredibly difficult to obtain for these groups, which led to the decision of using ultra-conserved elements (UCE) for elucidating species-level relationships within these groups.

In the final Chapter, a discussion of the previous five is undertaken.

Research Summary

The North America Southwest is home to a remarkable menagerie of flora and fauna with astonishing adaptations to arid climates. Nocturnal wasps are animals that are both exceptionally unique and especially informative. Chyphotidae is a key player in the desert biome of the United States. With a high level of mystique these nocturnal wasps warrant increased attention from the scientific community. I intend to give them the attention they deserve by using them in my research to help resolve questions that have remained unanswered for years. While there is always a debate as to the true age of mountain orogeny, and the subsequent rain-shadow desertification that formed the deserts we know today, there is potential for these unique creatures to help resolve these issues. Revising the taxonomy of both the males and females of this group will help make them ideal for use in phylogenetic and biogeographic analyses. By examining patterns of widespread species in *Chyphotes* and in the brachycistidines, as well as the entire family Chyphotidae, and by using them in conjunction with other unrelated nocturnal wasps, patterns can be seen that will show us origins, dispersal events, geological isolation events, and timing of these events. In particular, I hope this research contributes to the

understanding of the evolution of the desert biome in the United States. If nothing else, I hope this to be a first step at narrowing the range of dates that can be attributed to mountain orogeny and desertification events.

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CHAPTER 2

REASSESSING SPECIES BOUNDARIES IN THE BLACK-HEADED NOCTURNAL WASP SPECIES OF THE SUBGENUS *CHYPHOTES* BLAKE (HYMENOPTERA: CHYPHOTIDAE)[1]

Abstract

Although the taxonomy of *Chyphotes* (Hymenoptera: Chyphotidae) was revised by Mickel (1967), a great deal of taxonomic confusion remains in this complex group of nocturnal wasps. One challenging group of species has a distinct color pattern where the head is black contrasting with the reddish-brown body. This group is in the nominal subgenus *Chyphotes* (*Chyphotes*), and includes *C. aenigmus* Mickel, *C. atriceps* Mickel, *C. calexicensis* Bradley, *C. incredulus* Mickel, and *C. melaniceps* (Blake). Prior to Mickel (1967), authors thought that all of these were a single species (*Chyphotes melaniceps* (Blake)) due to their similar morphology and the overlap in their geographical distributions. We investigate the validity of these black-headed species with a comparison of morphology and sequence data for mitochondrial cytochrome c oxidase subunit I (COI). We obtained morphological data and sequences for all five species of black-headed *Chyphotes* (*Chyphotes*) and for a sixth black-headed species *C. ciaran* Sadler and Pitts, **sp. nov.** We also obtained sequence data for five additional species in the subgenus of *Chyphotes* and for five species from the subgenus *Pitanta*. These black-headed species

[1] This manuscript has been submitted for publication in *Annals of the Entomological Society of America* and was coauthored by J.P. Pitts and J.S.Wilson. Permission has been granted by the required coauthors for this research to be included in my dissertation (Appendix A).

are valid, based on differences in genitalic structures—albeit minor differences that would not denote species in other aculeate groups—and pairwise distances with interspecific variation being above 4% and intraspecific variation being below 3%. Additionally, Mickel's (1967) external morphological differences are unusable and no external set of characters was found making species recognition difficult. Diagnoses and updated distributions are provided for each species.

Key words: Sonoran Desert, Mojave Desert, USA, aculeate Hymenoptera

Chyphotidae (Hymenoptera) is little studied family of aculeate wasps that is restricted to the New World. The natural history of this family is unknown, but they are expected to be parasitoids, and, given their relationship to other aculeate families (e.g. Pilgrim *et al.* 2008; Branstetter *et al.* 2017), are likely parasitoids of beetles. Brothers and Finnamore (1993), however, suggested they parasitize camel spiders (Solifugae) based on non-peer-reviewed data. The family is comprised of two subfamilies Chyphotinae and Typhoctinae (Pilgrim *et al.*, 2008). Species of Typhoctinae are diurnal and rare, ranging throughout the New World. Chyphotinae contains a single genus, *Chyphotes* Blake, which includes all the nocturnal species, and can be found from Southern Canada to Northern Mexico with the majority of species occurring in the southwestern United States.

The genus *Chyphotes* has been divided into two subgenera, the nominal subgenus and *Pitanta* Pate (Mickel 1967). *Pitanta* species are typically smaller that *Chyphotes s.s.*

and have characteristic genitalia. Mickel (1967) designated seven species-groups in *Pitanta* based on both wing venation and genitalic characters. For *Pitanta* species, he observed a variety of different genitalic characteristics, and noted both hooked and peg-like spines at the base of the digitus, as well as the rounded or acute shapes of the basiparamere. He only used the overall shape of parameres for the *C.* (*P.*) *attenuatus* species-group where the most striking examples exhibit reflexed margins of the parameres. *Chyphotes s.s.* species seem to have more conserved morphology and, as such, are more difficult to discriminate. Mickel (1967) was unable to place the *Chyphotes s.s.* species into species-groups, and, although mentioned in his descriptions, he did not use genitalic characters to discriminate species. This is strange given that Buzicky (1941) showed how useful genitalia are for species-level identification in *Chyphotes s.s.* with paramere shape being by far the best way to establish identifications.

Within the subgenus *Chyphotes*, males of species with a black head are particularly challenging to distinguish and, unfortunately, represent some of the most abundant of the *Chyphotes* species. These species include *C. aenigmus* Mickel, *C. atriceps* Mickel, *C. calexicensis* Bradley, *C. incredulus* Mickel, and *C. melaniceps* (Blake). The males of these species have a distinct color pattern, in which the head is almost entirely black and contrasts with the body that is reddish-brown, and is unique to these species for the subgenus. The first black-head species described was *C. melaniceps* (Blake 1886). In 1967 Mickel revised the genus and split *C. melaniceps* into five different species based on body coloration and spacing of the ocelli. Mickel illustrated the genitalia of these species, but did not use these structures for separating the species with one

exception. He used the minor differences in the digitus for helping to separate *C. atriceps* and *C. calexicensis.* This genitalic character seems to be unreliable and includes both its length (long versus short) and the shape of the inner margin (sinuate versus arcuate). Subsequently, the external characters Mickel employed to separate these species have proven unreliable given the considerable overlap of the characters between multiple black-headed species. Due to the seeming lack of consistent external morphological characters, we question if it was appropriate to split these wasps into five separate species such as Mickel (1967) concluded.

The purpose of this study is to reconsider the validity of the black headed species of the subgenus *Chyphotes* using new morphological and molecular data. To address this question, morphological characters, such as male genitalia, were studied to determine better character systems for separating species. After species limits were determined, the validity of Mickel's external morphological characters were tested. Genitalic diagnoses and new distributional records are provided for the valid black-headed species.

Materials and Methods

Field Collection

Materials used were specimens collected between 2005 and 2014 by light traps. Light traps consist of a fluorescent camping lantern and small bowls filled with non-toxic soapy water. All specimens were stored in 95% ethanol to preserve DNA for molecular analyses until they were dried and pinned. Any specimen used for molecular work has been labeled as voucher specimens and deposited in the Entomological Museum of Utah State

University (EMUS). All primary types examined were compared with vouchers to assure correct identification.

Taxon Sampling

All five black-headed species and one novel morphospecies based on novel genitalic characters were examined during this study totaling 4,058 specimens plus type material. To determine the level of variation between species in COI we included five additional species from the subgenus *Chyphotes* (*C. belfragei* (Blake)*, C. capitatus* Mickel*, C. mandibularis* Mickel, *C. mexicanus* Mickel, and *C. peninsularis* Fox), and five species from the subgenus *Pitanta* (*C. bruscus* Buzicky, *C. minimus* Mickel, *C. mojave* Pate, *C. nubeculus* (Cresson)*,* and *C. subulatus* Buzicky). Numbers of specimens studied from each state are given. New state records are indicated by *. In some cases, states are listed in which zero specimens were studied. This means that Mickel (1967) published records from these localities previously, but these specimens were not studied here nor were additional specimens from these regions seen for this study.

Morphological Methods

Pinned specimens representing all species included in this study and including type material have been examined for morphological characters as outlined by Mickel 1967, as well as novel characters based on genitalic morphology. All specimens were examined using a high power dissecting microscope, any dissections were performed under a microscope using a minuten pin. We examined genitalia of 4,058 black-headed males,

which include multiple specimens of all species concerned in this study. These genitalia were either mounted on points that were attached to the pin, or in the case of illustrations or types, they were placed in genitalia capsules with glycerin. This includes materials from eight states in the USA and one state in Mexico collected between the years 1970 and 2016.

Acronyms for collections from which specimens were borrowed are:

ANSP—Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

CASC—Department of Entomology, California Academy of Sciences, San Francisco, California, USA.

CUIC—Cornell University, Ithaca, New York, USA.

EMUS—Entomological Museum of Utah State University, Logan, Utah, USA.

UMSP—University of Minnesota Insect Collection, St. Paul, Minnesota, USA.

Molecular Methods

Protocols for molecular methods were followed as outlined by Pilgrim and Pitts (2006). DNA from two specimens for all five species of black-headed *Chyphotes* and the sixth morphospecies based on novel genitalic characters was obtained using a High Pure PCR Template Preparation Kit (Roche Applied Science, Indianapolis, IN); five additional species in the subgenus of *Chyphotes,* and five species from the subgenus *Pitanta* from one specimen each were analyzed as well. Each specimen was used in its entirety during extraction, no body parts were removed and no additional holes were made in the mesosoma, which maintains morphological features for future taxonomic use. PCR was

used to amplify the gene Cytochrome c oxidase subunit 1 (COI). Sequences were run in both forward and reverse directions and combined using Geneious version 9.0.2 (Kearse *et al*., 2012). Genetic distances between species were calculated in the program Geneious as pairwise percentages.

Results

Morphological Results

Study of holotypes and their genitalia reveal diagnostic genitalic characters not indicated by Mickel (1967). These are outlined in the taxonomic section for each species. The external morphological characters proposed by Mickel to separate the black-headed species were found to be largely inaccurate. The first character used by Mickel (1967) to differentiate *C. melaniceps* from the remaining four species was the coloration of the third metasomal tergum. Mickel states that *C. melaniceps* is the only species that supposedly has a tergum that is concolorous with the remainder of the body, while the other species supposedly exhibit a darkened third metasomal tergum. Specimens based on molecular data and genitalic morphology of *C. melaniceps* exist, however, that have a darkened third metasomal tergum while other black-headed species exist that have a concolorous third metasomal tergum. Mickel (1967) also used ocellocular distance measurements, sternal depressions and degree of punctuation to classify the remaining four species (Mickel, 1967). Measurements made on 32 specimens, eight of each of the four species based on molecular data and genitalic morphology, resulted in all species having similar and overlapping values, falling within the same narrow range. Thus, these

characters are useless for determination of these species. Lastly, species have been identified based on collection locale alone. Mickel (1967) created distribution maps for a number of *Chyphotes* species, including the species in question. In many groups of insects using geographical distributions to determine one species from another can be a useful diagnostic tool. Unfortunately, this is not the case for these species as they all have overlapping distributions, and are often collected at the same time and rate.

Molecular Results

The final alignment encompassed an average of 614 base pairs for COI for all six black-headed species. All of the black-headed species differed by at least 4% in pairwise genetic distances, but most by 6.8% or more, while intraspecific variation is 3% or less (Table 2.1).

Taxonomy

***Chyphotes* (*Chyphotes*) *aenigmus* Mickel, 1967**

Chyphotes (*Chyphotes*) *aenigmus* Mickel, 1967, *Trans. Amer. Ent. Soc.* 93:147-148, male.

Table 2.1. Genetic distances for COI with the black-headed species in bold

	C. (C.) aenigmus (N=2)	***C. (C.) atriceps*** (N=2)	*C. (C.) belfragei* (N=1)	***C. (C.) calexicensis*** (N=2)	*C. (C.) capitatus* (N=1)	***C. (C.) ciaran sp. nov.*** (N=2)	***C. (C.) incredulus*** (N=2)	*C. (C.) mandibularis* (N=1)	***C. (C.) melaniceps*** (N=2)	*C. (C.) mexicanus* (N=1)	*C. (C.) peninsularis* (N=1)	*C. (P.) bruscus* (N=1)	*C. (P.) minimus* (N=1)	*C. (P.) mojave* (N=1)	*C. (P.) nubeculus* (N=1)	*C. (P.) subulatus* (N=1)
C. (C.) aenigmus (N=2)	2.9	10.1-11.0	10.7-11.5	10.3-10.9	10.6-11.5	11.7-12.5	10.4-10.8	8.8-10.0	9.1-9.8	8.6-9.7	10.6-11.8	15.7-16.0	17.5-17.8	16.3-16.7	18.3-18.6	16.5-17.1
. (C.) atriceps (N=2)	10.1-11.0	2.4	9.8-9.9	10.7-11.7	9.6-10.1	11.9-12.6	8.5-8.6	8.0-8.6	8.3-10.2	9.3-9.4	10.1-10.3	17.6	18.7-19.1	16.9-17.4	17.1-17.6	16.4-17.1
C. (C.) belfragei (N=1)	10.7-11.5	9.8-9.9	--	9.3-9.4	10.1	10.1	9.0-9.6	8.5	8.1-9.4	9.0	11.2	16.4	19.2	16.4	18.6	18.2
C. (C.) calexicensis (N=2)	10.3-10.9	10.7-11.7	9.3-9.4	0.8	10.1-10.6	4.5-5.7	8.8-9.8	8.6-8.8	8.5-9.8	8.5-8.6	10.3-10.7	15.5-15.6	18.7-18.9	16.9	18.9-19.1	17.4-17.8
C. (C.) capitatus (N=1)	10.6-11.5	9.6-10.1	10.1	10.1-10.6	--	11.2-11.4	10.3	8.0	9.1-9.9	9.8	6.5	17.1	19.9	17.4	19.4	18.9
C. (C.) ciaran sp. nov. (N=2)	11.7-12.5	11.9-12.9	10.1	4.5-5.7	11.2-11.4	2.0	10.3-10.7	9.1-9.3	9.6-10.6	8.5-9.3	12.1-12.4	16.7-16.9	19.6-19.7	17.6-17.8	19.9	18.2
C. (C.) incredulus (N=2)	10.4-10.8	8.5-8.6	9.0-9.6	8.8-9.8	10.3	10.3-10.7	3.1	6.5-6.7	6.8-8.2	8.3-9.1	9.0-9.6	16.4-17.3	18.2-19.1	16.6-17.6	17.9-19.2	16.0-16.8
C. (C.) mandibularis (N=1)	8.8-10.0	8.0-8.6	8.5	8.6-8.8	8.0	9.1-9.3	6.5-6.7	--	6.0-7.2	6.8	9.0	15.6	19.7	16.8	18.6	17.8
C. (C.) melaniceps (N=2)	9.1-9.8	8.3-10.2	8.1-9.4	8.5-9.8	9.1-9.9	9.6-10.6	6.8-8.2	6.0-7.1	3.3	6.2-6.8	10.3-11.4	16.8-17.6	19.7-20.2	16.6-17.1	19.7-20.7	18.7-19.1
C. (C.) mexicanus (N=1)	8.6-9.7	9.3-9.4	9.0	8.5-8.6	9.8	8.5-9.3	8.3-9.1	6.8	6.2-6.8	--	10.7	16.1	19.2	16.6	18.6	16.8
C. (C.) peninsularis (N=1)	10.6-11.8	10.1-10.3	11.2	10.3-10.7	6.5	12.1-12.4	9.0-9.6	9.0	10.3-11.4	10.7	--	17.1	19.7	17.1	19.1	18.7
C. (P.) bruscus (N=1)	15.7-16.0	17.6	16.4	15.5-15.6	17.1	16.7-16.9	16.4-17.3	15.6	16.8-17.6	16.1	17.1	--	14	13	12.1	13.8
C. (P.) minimus (N=1)	17.5-17.8	18.7-19.1	19.2	18.7-18.9	19.9	19.6-19.7	18.2-19.1	19.7	19.7-20.2	19.2	19.7	14.0	--	10.9	14.8	14.2
C. (P.) mojave (N=1)	16.3-16.7	16.9-17.4	16.4	16.9	17.4	17.6-17.8	16.6-17.6	16.8	16.6-17.1	16.6	17.1	13.0	10.9	--	12.7	11.9
C. (P.) nubeculus (N=1)	18.3-18.6	17.1-17.6	18.6	18.9-19.1	19.4	19.9	17.9-19.2	18.6	19.7-20.7	18.6	19.1	12.1	14.8	12.7	--	12.1
C. (P.) subulatus (N=1)	16.5-17.1	16.4-17.1	18.2	17.4-17.8	18.9	18.2	16.0-16.8	17.8	18.7-19.1	16.8	18.7	13.8	14.2	11.9	12.1	--

Diagnosis of male. This species can be separated from other species in this subgenus by the presence of darkened integument of the head and the characteristic genitalia where the dorsal and ventral margins of paramere are divergent, curvature of dorsal margin more abrupt than ventral margin, being widest subapically to submedially, with the apical margin being broadly rounded, and with the basal area of the dorsal and ventral margins with a pronounced bend dorsally. A dorsal patch of somewhat anteriorly directed setae is present near the widest portion of the paramere (Figs 2.1, 2.2).

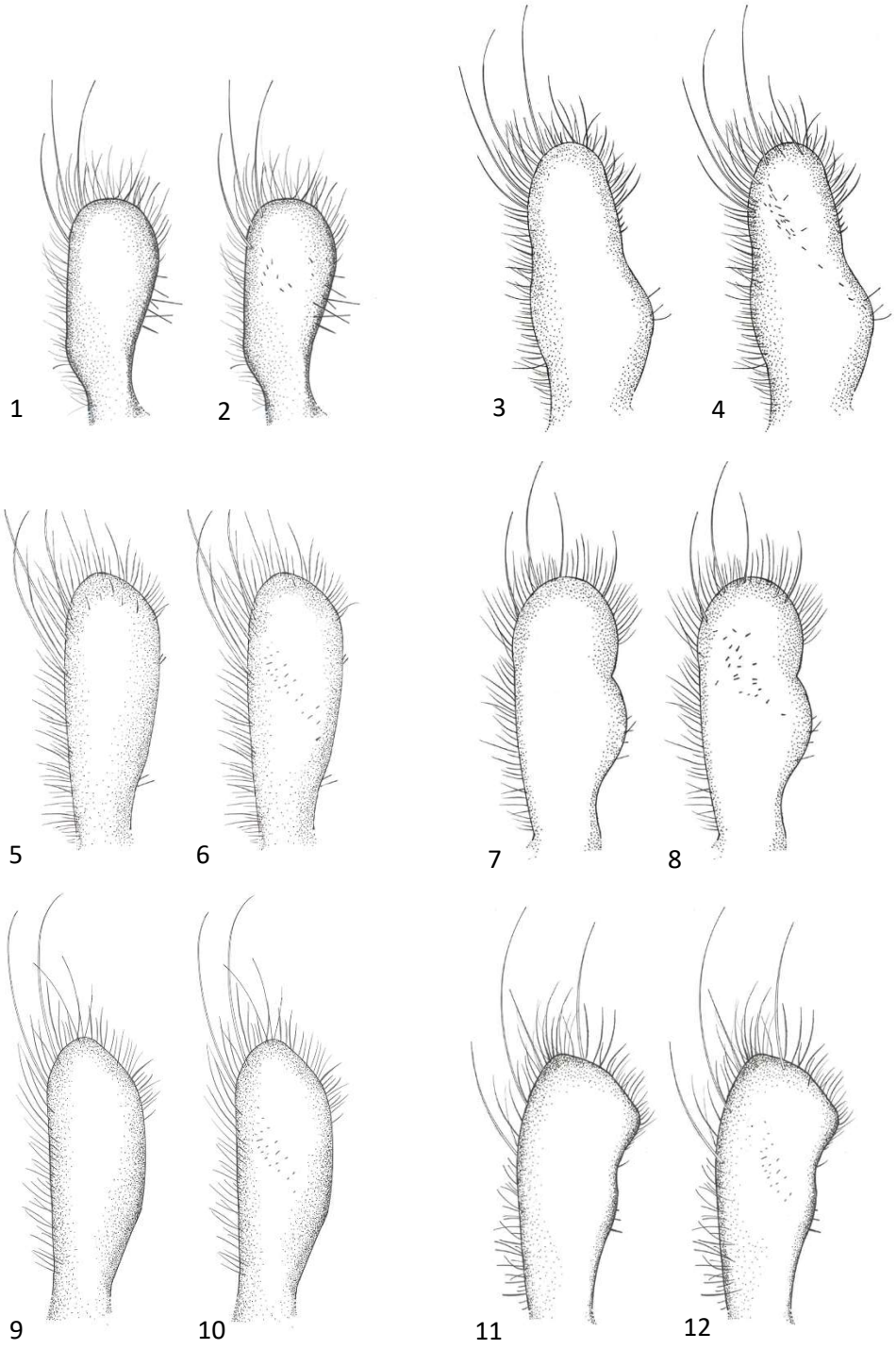
Female. Unknown.

Material Examined and Distribution. *Holotype*. Arizona, Pima, Co., Tucson, 4.May.1962, C.E. Mickel (UMSP). *Further specimens examined*: USA: Arizona (148 specimens), California (474 specimens), *Nevada (413 specimens), *New Mexico (19 specimens), *Utah (43 specimens); Mexico: Sonora (0 specimens).

***Chyphotes* (*Chyphotes*) *atriceps* Mickel, 1967**

Chyphotes (*Chyphotes*) *atriceps* Mickel, 1967, *Trans. Amer. Ent. Soc.* 93:134-135, male.

Diagnosis of male. This species can be separated from other species in this subgenus by the presence of darkened integument of the head and the characteristic genitalia where the paramere is widest submedially to medially, the distal half of paramere narrows dorsally with a broadly rounded apex with the overall appearance being reminiscent of a bowling pin (Figs 2.3, 2.4).



Figs 2.1-2.12. Paramere of male genitalia, outer face, inner face; 1, 2. *Chyphotes aenigmus*; 3, 4. *C. atriceps*; 5, 6. *C. calexicensis*; 7, 8. *C. ciaran*, **sp. nov.**; 9, 10. *C. incredulus*; and 11, 12. *C. melaniceps*.

Female. Unknown.

Material Examined. *Holotype*. Arizona, Pima Co., Sonora Desert Museum, 21-24.Aug.1962, W.L. Nutting and S. Oman (UMSP). *Further specimens examined*: USA: Arizona (96 specimens), *California (301 specimens), Idaho (8 specimens), Nevada (167 specimens), New Mexico (14 specimens), Texas (57 specimens), Utah (70 specimens), Washington (1 specimen); Mexico: Chihuahua (0 specimens), Sonora (0 specimens).

***Chyphotes* (*Chyphotes*) *calexicensis* Bradley, 1917**

Chyphotes calexicensis Bradley, 1917, *Trans. Amer. Ent. Soc.*, 43:284, fig 1, male.
Chyphotes calexicensis Buzicky, 1941, *Ent. Amer*., 21 (n.s):220, male.
Chyphotes calexicensis Krombein, 1951, *U.S.D.A. Monograph* 2:750, male.
Chyphotes (*Chyphotes*) *calexicensis* Mickel, 1967, *Trans. Amer. Ent. Soc.* 93:144-145, male.

Diagnosis of male. This species can be separated from other species in this subgenus by the presence of darkened integument of the head and the characteristic genitalia where the dorsal and ventral margins of the paramere widens gradually to the apex which is rounded and the overall appearance is spoon shape, the dorsal margin is entire to slightly interrupted medially, while the ventral margin is entire, and the apex is broadly rounded to slightly flattened (Figs 2.5, 2.6).

Female. Unknown.

Material Examined. *Holotype*. California, Calexico, 11.Aug.1914, J.C. Bradley (CUIC: Type no. 127.1). *Further specimens examined*: USA: Arizona (142 specimens), California (112 specimens), *Nevada (229 specimens), *Texas (1 specimen), *Utah (3 specimens); Mexico: Sonora (3 specimens).

***Chyphotes* (*Chyphotes*) *ciaran* Sadler and Pitts, sp. nov.**

Diagnosis. This species can be separated from other species in this subgenus by the presence of darkened integument of the head and the characteristic genitalia where the paramere has the dorsal margin interrupted medially, distinctly bilobate, while the ventral margin entire, and the apex is broadly rounded (Figs 2.7, 2.8).

Description of male. *Coloration:* Head black, except anterior margin of front, clypeus and proximal two-thirds of mandibles, testaceous, remainder of mandible ferruginous; mesosoma and metasoma testaceous, except third abdominal tergum slightly darker than remaining terga; antennae and legs stramineous; head clothed with sparse, erect and appressed, pale yellowish setae; mesosoma clothed throughout with sparse, mostly erect, pale yellowish setae; legs clothed with sparse, pale yellowish setae; wings hyaline with fuscous cloud beyond marginal and submarginal cells.

Head: Mandibles with dorsal and ventral carinae weak, inconspicuous, equal in width throughout their length, acuminate at tip and bidentate with small tooth near tip; clypeus with moderate, close punctures; front and vertex nitid, with small punctures

separated by distance at least equal to their width; ocellocular distance equal to 1.25x length of lateral ocellus.

Mesosoma: Pronotum and mesonotum with moderate punctures, distance between punctures much less than their diameter; scutellum with moderate close punctures; propodeum reticulate, median dorsal area and lateral area narrow reticulate, posterior face becoming more broadly reticulate; mesopleura with moderate punctures; mesosternum with small sparse punctures, each area laterad of median line evenly convex, medial groove closed anteriorly by pair of horizontal teeth whose apices meet on median line; posterior margin of mesosternum with erect tooth in front of each middle coxa; metasternum with median, longitudinal carina and nitid on each side of carina; posterior margin of metasternum with small, erect tooth in front of each hind coxa.

Wings: Two submarginal and two discoidal cells, second recurrent vein received by second submarginal cell before its middle.

Metasoma: Dorsal face of first sternum one half length of first tergum, rugoso-punctate; first tergum with large, shallow, more or less confluent punctures; second tergum with large, slightly elongate, somewhat confluent punctures anteriorly, punctures becoming slightly smaller from front to rear in lateral areas, and smaller, more separated and distinct from front to rear in median area; posterior margin sparsely punctate; interpunctal areas nitid; remaining terga with small, sparse punctures and nitid to slightly shagreened; ventral face of first sternum coarsely rugoso-punctate, except anterior one-fifth nitid, weakly punctate; second sternum coarsely rugoso-punctate anteriorly, punctures becoming progressively smaller, shallower and more separated from front to

rear, posterior margin with sparse, small punctures; second sternum with median, ovate, shallow, concave area on posterior two-thirds, concavity not extending to posterior margin; remaining sterna nitid to slightly shagreened with small, well separated punctures.

Genitalia: Lateral margins of aedeagus entire, not serrate; dorsal margin of paramere interrupted medially, distinctly bilobate; ventral margin of paramere entire; apex of paramere broadly rounded; digitus approximately 0.33X length of paramere with inner margin weakly arcuate (Figs 2.7, 2.8).

Length: 12.3 mm, range 9.5-13.2 mm.

Female. Unknown.

Material Examined. *Holotype*. **Utah**, *Washington Co.,* Beaver Dam Slope, 5 mi N Beaver Dam, male, 2-3.Jun.2007, J.P. Pitts, J.S. Wilson, and K.A. Williams (EMUS). *Paratypes*: **Arizona**: *Cochise Co*., Cavot Rd., 0.5 mi W stateline, 2 males, 19-20.May.2009, 1 male, 10.Aug.2009, 1 male, 12-13.Aug.2009, K.A. Williams (EMUS); *Maricopa Co*., Vekol Wash, 5 km N I-8 at Vekol Rd, 1 male, 25.May-3.Jul.2010, M.E. Irwin (EMUS); *Mojave Co.*, Black Rock Rd., 1 male, 1-2.Jun.2007, J.P. Pitts, J.S. Wilson, and K.A. Williams (EMUS). **California**: *Riverside Co*., Joshua Tree National Park, 3 males, Jul.2012, 2 males, Sep.2012, E.A. Sadler (EMUS); *San Bernardino Co*., 5.5 mi S Barstow, HWY 247, 2 males, 25.Jul.2006, K.A. Williams (EMUS). **Nevada**: *Nye Co.*, Ash Meadows National Wildlife Refuge: Creosote Dune, 2 males, 13-14.May.2009, 2 males, 19-20.Sep.2009, N. Boehme (EMUS); Crystal Atriplex Dune, 1 male, 10Jun.2009, N. Boehme (EMUS); Crystal Mesquite Dune, 1 male, 13-29.Jun.2009,

1 male, 5-6.Aug.2009, 1 male, 18-19.Sep.2009, N. Boehme (EMUS); Isolated Dune, 4 males, 24-25.Jun.2009, N. Boehme (EMUS); Moon Scape nr Isolated Dune, 1 male, 24-25.Jun.2009, N. Boehme (EMUS); Peterson Dune, 1 male, 22-23.Jul.2009, N. Boehme (EMUS); School Springs, 3 males, 9.Jun.2009, 1 male, 23-24.Jun.2009, 1 male, 19-20.Sep.2009, N. Boehme (EMUS); Spring Road, 1 male, 9.Jun.2008, J.P. Pitts (EMUS); South Spring Meadows, 1 male, 24-25.Jun.2009, 1 male, 6-7.Jul.2009, 1 male, 5-6.Sep.2009, N. Boehme (EMUS). **Texas**: *Brewster Co*., Big Bend Ranch SP, 27 mi E Presidio, 1 male, 16-17.May.2008, J.S. Wilson and K.A. Williams (EMUS).**Utah**, *Washington Co.,* Beaver Dam Slope, 5 mi N Beaver Dam, 3 males, 2-3.Jun.2007, J.P. Pitts, J.S. Wilson, and K.A. Williams (EMUS).

Etymology. The name ciarán means “little dark-haired one” in Gaelic. Treat as a noun in apposition.

***Chyphotes* (*Chyphotes*) *incredulus* Mickel, 1967**

Chyphotes (*Chyphotes*) *incredulus* Mickel, 1967, *Trans. Amer. Ent. Soc.* 93:149-150, male.

Diagnosis of male. This species can be separated from other species in this subgenus by the presence of darkened integument of the head and the characteristic genitalia where the paramere has the dorsal margin diverging from the ventral margin from the base to approximately half the length of the paramere, such that the paramere becomes widest

roughly half the distance from the base. The dorsal margin becomes parallel with the ventral margin afterwards, and the apex is broadly rounded (Figs 2.9, 2.10).

Female. Unknown.

Material Examined. *Holotype*. Mexico, Chihuahua, Santa Clara Canyon, 5 mi. W Parrita, 6.Jun.1954, J.W. MacSwain and E.I. Schlinger (CASC). *Further specimens examined*: USA: *Arizona (318 specimens), *California (188 specimens), *Nevada (487 specimens), New Mexico (112 specimens), Texas (42 specimens), *Utah (4 specimens); Mexico: Chihuanhua (0 specimens), Nuevo Leon (0 specimens).

Remarks. Mickel (1967) provided a poor illustration of the genitalia of this species (fig 15: Mickel 1967). The illustration does not match the holotype or species making the genitalic morphology look more similar to *C. calexicensis* than it really is.

***Chyphotes* (*Chyphotes*) *melaniceps* (Blake, 1886)**

Photopsis melaniceps Blake, 1886, *Trans. Amer. Ent. Soc*., 13:264, male.

Mutilla melaniceps Dalla Torre, 1897, *Cat. Hymen*., 8:60, male.

Chyphotes melaniceps Fox, 1899, *Trans. Amer. Ent. Soc*., 25:277, male.

Chyphotes melaniceps André, 1903, *Gen. Ins.,* 11:11, male.

Chyphotes piceiceps Baker, 1905, *Invertebrata Pacifica*, 1:116, male. Synonymized by Buzicky (1941).

Chyphotes melaniceps Buzicky (in part), 1941, *Ent. Amer.,* 21 (n.s.):220, male.

Chyphotes melaniceps Krombein, 1951, *U.S.D.A. Monograph* 2:750, male.

Chyphotes (*Chyphotes*) *melaniceps* Mickel, 1967, *Trans. Amer. Ent. Soc.* 93:141-142, male.

Diagnosis of male. This species can be separated from other species in this subgenus by the presence of darkened integument of the head and the characteristic genitalia where the paramere margins are divergent from base being widest distally, dorsal margin interrupted towards apex, and apex is truncate to slightly rounded (Figs 2.11, 2.12).

Female. Unknown.

Material Examined. *Holotype*. Arizona (ANSP: Type no. 4591). *Further specimens examined*: USA: Arizona (251 specimens), California (408 specimens), Nevada (194 specimens), *New Mexico (1 specimen), *Texas (2 specimens), Utah (327 specimens); Mexico: Baja California (0 specimens).

Discussion

These analyses suggest that the group of black-headed *Chyphotes* includes six distinct species, one of which is new to science and is described here. The validity of the species is based on distinct, but minor, morphological differences in genitalia. The validity of these species and the novel genitalic characters determined in this study also are supported by molecular data where each of the species differed by at least 4% in pairwise genetic distances (Table 2.1). The difficulty in finding easily describable genitalic characters likely is what led Mickel (1967) to further examine and completely rely on external morphology. Unfortunately, Mickel's external morphological characters

are completely unreliable and the only consistent way to discriminate these species is with these same minor differences in genitalic structure. Many of the black-headed specimens can be distinguished based on genitalia with little difficulty. The other half must be examined closely, because of the low level of genitalic variation between some of the species (i.e., *C. calexicensis* and *C. incredulus*). In some relatively rare instances, the genitalia may resemble a form seemingly between two species making identifications exceedingly difficult or impossible unless a series of specimens from the same locale are available for study. Despite the difficulty, genitalia currently are the only character from which accurate identifications can be made, and in other groups these subtle differences would not be considered enough evidence to denote new species.

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CHAPTER 3

NOCTURNAL VELVET ANTS (HYMENOPTERA: MUTILLIDAE) OF JOSHUA TREE NATIONAL PARK, RIVERSIDE COUNTY, CALIFORNIA WITH THE DESCRIPTION OF THREE NEW SPECIES[2]

Abstract

The diversity of nocturnal velvet ants at Joshua Tree National Park (JTNP) is investigated along with seasonal activity. The diversity of velvet ants found at JTNP is compared to the diversity of velvet ants found at the Algodones Sand Dunes, Philip L. Boyd Deep Canyon Desert Research Center, Ash Meadows National Wildlife Refuge and the Nevada Test Site. Diagnoses and a key are provided for the velvet ants of JTNP. Forty-one species in six genera, based on 10,202 specimens collected from a transect of 14 sampling sites transitioning from the Mojave to the Sonoran deserts, are found to inhabit areas in and around the park. *Odontophotopsis dalyi, O. odontoloxia* and *Photomorphus schoenwerthi* are described as **new species**. *Odontophotopsis* (*Odontophotopsis*) *ambigua* Mickel (1983) is a junior synonym of *O. delodonta* Viereck (1904), **new synonym**. The females of too few of the species are known, so only the males are treated. A key to all of the species and illustrations for those species not previously illustrated are provided for the males.

[2] This manuscript has been submitted for publication in *Zootaxa* and was coauthored by J.P. Pitts and J.S.Wilson. Permission has been granted by the required coauthors for this research to be included in my dissertation (Appendix A).

Key words: Sonoran Desert, Mojave Desert, USA

Introduction

Velvet ants (Mutillidae: Hymenoptera) are a family of wasps that has species endemic to the deserts of North America. However, the nocturnal velvet ant fauna of JTNP is poorly known. Velvet ant females parasitize the larval or pupal stages of holometabolous insects, such as Diptera, Coleoptera and Hymenoptera, with most known hosts being aculeate Hymenoptera (Brothers *et al.* 2000). Only sparse natural history information exists for most species of velvet ants. Presumably, female velvet ants spend much time underground searching for hosts, and in most areas females of nocturnal species are less frequently encountered than males. Males of nocturnal velvet ant species are more often encountered as they are attracted to light traps.

Significant sampling of velvet ants has never occurred in Joshua Tree National Park (JTNP). This park is large, covering 3,199.59 km^2 of land and includes both the Mojave and Sonoran deserts of southeastern California. Each of these deserts is defined principally by elevation. The Mojave Desert is higher in elevation than the Colorado Desert portion of the Sonoran Desert. The park is named after one of the most the common and recognizable plants found in the Mojave Desert portion of the park, the Joshua tree (*Yucca brevifolia*). Other plants ubiquitous to this desert are piñon pine species, California juniper (*Juniperus californica*), desert scrub oak (*Quercus turbinella*), Tucker's oak (*Quercus john-tuckeri*) and Muller oak (*Quercus cornelius-*

mulleri) (Ricketts *et al.* 1999). The Colorado Desert, which occurs below 3,000 feet (910 m), has flora such as Creosote bush (*Larrea tridentata*), scrub Ocotillo (*Fouquieria splendens*), desert Saltbush (*Atriplex* spp.), *Yucca* and Cholla cactus (*Cylindropuntia bigelovii*) (Ricketts *et al.* 1999).

The objectives of this study are to determine what species of nocturnal velvet ant species exist at JTNP, if there are faunal differences between the different deserts of the park, and to provide a means for identifying those species using diagnoses and keys. Because the park is situated at the transition zone between two deserts, specimens were collected in a transect from both deserts. We also discuss the potential for additional species to be found at the park and speculate on which additional species may occur there by the comparison of the JTNP species and those species found at the Algodones Sand Dunes and Philip L. Boyd Deep Canyon Desert Research Center (Pitts *et al.* 2009, 2010a), both of which are situated in the Sonoran Desert, and Ash Meadows National Wildlife Refuge (AMNWR) and the Nevada Test Site (NTS) (Ferguson 1967; Allred 1973; Boehme *et al.* 2012), situated in the Mojave Desert. This type of comparison has been done previously (Wilson *et al.* 2010), but this study was preliminary and was based on too few specimens. This comparison is also made to better understand what species are restricted to a given desert for their potential use in historical biogeography analyses of the southwestern USA.

Materials and Methods

Collecting methods and design of transect

Within Joshua Tree National Park, Pinto Basin Road served as the perfect transect between the Mojave and Sonoran Deserts. Beginning at the park boundary at the North Entrance and continuing south to the Cottonwood Visitor Center, light traps where set up approximately every three miles (Table 3.1). Trapping along Pinto Basin Road provided a 27 mile transect with a 2,386 foot change in elevation. This allowed for five light traps to be placed in the Mojave Desert; the sites of these traps are designated N9, N7, N5, N3 and N1, where N stands for north of the transition zone and the number represents the distance from the transition zone in miles. This also allowed for one trap in the transition zone (T) and eight traps south of the transition zone in the Sonoran Desert (S1, S3, S5, S7, S9, S11, S13 and S18). Once again, where S stands for south of the transition zone and the number represents the distance from the transition zone in miles.

Specimens were collected along the transect with light traps. The light traps consisted of a fluorescent battery-powered camping lantern and small bowls filled with slightly soapy water. Typically, only males were collected by the light traps. Traps were deployed at dusk and collected at dawn. There were four sampling periods starting in July and continuing through October of 2012 (18-21 July, 26-28 August, 22-24 September, 26-28 October). During each sampling event, specimens were collected each evening for a total of two to three nights. All collected specimens were stored in 95% ethanol to preserve DNA for molecular analyses. GPS locations were determined for each collection site (Table 3.1).

Table 3.1. Transect site information.

Site Name	Site Location	Distance From Road Edge (ft)	Elevation (ft)	Dominant Vegetation Type
N9	N34.00482 W116.04924	218	4,160	Joshua Tree
N7	N34.02017 W116.01778	290	3,646	Yucca & Joshua Trees
N5	N33.99412 W116.02134	296	3,914	Yucca & Joshua Trees
N3	N33.97477 W115.99798	196	3,444	Yucca & Creosote
N1	N33.95148 W115.98084	248	2,953	Creosote & Cheesebush
T	N33.94111 W115.96973	193	2,761	Creosote, Mesquite, & Smoke tree
S1	N33.93315 W115.95633	183	2,540	Smoke tree
S3	N33.92409 W115.92458	104	2,069	100% Jumping Cholla
S5	N33.92419 W115.92508	183	1,834	Small Creosote
S7	N33.91169 W115.86460	232	1,774	Small Creosote & Cheesebush
S9	N33.90141 W115.83225	211	1,784	Small Creosote
S11	N33.87896 W115.81215	253	1,993	Creosote & Mormon tea
S13	N33.85631 W115.79056	181	2,231	Creosote
S18	N33.80103 W115.78088	203	2,793	Creosote

Taxonomic methods

All specimens collected at JTNP during the transect are deposited in the Department of Biology Insect Collection, Utah State University, Logan, UT (EMUS).

Codens for collections from which specimens were borrowed are:

ANSP – Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

BMNH – The Natural History Museum, London, United Kingdom.

CASC – Department of Entomology, California Academy of Sciences, San Francisco, California, USA.

CDFA – California State Collection of Arthropods, Sacramento, California, USA.

CISC – Essig Museum of Entomology, Department of Entomological Sciences, University of California, Berkeley, California, USA.

CUIC – Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, New York, USA.

EMUS – Department of Biology Insect Collection, Utah State University, Logan, Utah, USA.

NMNH – National Museum of Natural History, Washington D.C., USA.

SEMC – Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.

UAIC – Department of Entomology Collection, University of Arizona, Tucson, Arizona, USA.

UMSP – University of Minnesota Insect Collection, St. Paul, Minnesota, USA.

All specimens were examined with a Leica S8APO stereomicroscope, and all measurements were made with an ocular micrometer. Mandibular ratios were calculated by dividing the width at the ventral tooth, the excision after the ventral tooth, and the greatest apical width by the width at the base of the mandibles. Male genitalia were dissected from the specimens by using minuten pins and placed in genitalia capsules with glycerin. Genitalia were observed with a light microscope and illustrated using a camera lucida.

We use the term “simple setae” for setae that are smooth and do not have barbed surfaces. “Brachyplumose setae” refers to setae with barbs that are less than or equal to the diameter of the shaft at the attachment of the barb. “Plumose setae” have longer barbs. We use the abbreviations T2, T3, etc., to denote the second, third, etc., metasomal terga while S2, S3, etc., denote the second, third, etc., metasomal sterna. MC is used as an abbreviation for marginal cell. The digitus or cuspis length relative to the free paramere length is used here to quantify differences in genitalic structure. For ease of comparison and to facilitate identification without dissecting the genitalic capsule, the cuspis, digitus, and paramere measurements are taken from the apical margin of the basal paramere lobe in dorsal view to the apex of each respective structure. This method facilitates making all measurements from the dorsal view. We use the term mesosternum to denote the venter of the mesosoma between the fore and mid coxa, which is actually a

horizontal extension of the mesopleura. To do otherwise would lead to further confusion in an already difficult group.

To keep the material examined sections concise, collection localities while the transect was in operation are abbreviated. Material examined from the transect is listed simply as JTNP followed by a date, such as 18–21.Jul.2012, and followed by the number of specimens from each site, such as 1 ♂ S13. Refer to Table 3.1 for exact locality data. Material examined from other institutions, type material, and specimens that were collected outside of operation of the transect are written out in full.

Results

From the transect, 43 species were collected at JTNP in 2012 totaling 10,202 specimens (Table 3.2). *Odontophotopsis microdonta* Ferguson (n=2195) and *O. clypeata* Schuster (n=1241) are the most abundant of all the species found at the park (Table 3.2). The rarest species, those with less than 10 individuals found throughout the course of the study, include *O. setifera* Schuster (8 specimens), *O. dalyi*, **sp. nov.** (5), *O. obscura* Schuster (3), *O. odontoloxia*, **sp. nov.** (2), *Photomorphus clandestina* (Viereck) (2), *Sphaeropthalma triangularis* (Blake) (2), *O. acmaea* Viereck (1), *O. aufidia* Mickel (1), *P. schoenwerthi*, **sp. nov.** (1), *S. militaris* Schuster (1), *S. nana* (Ashmead) (1) and *S. sublobata* Schuster (1). *Odontophotopsis setifera*, *S. nana*, *O. aufidia* were also considered rare according to surveys of the Ash Meadows National Wildlife Refuge (AMNWR) (Boehme *et al.* 2012). The nocturnal mutillid fauna of JTNP and AMNWR are compared in Table 3.2 and 3.3. Summaries and comparisons of mutillid species from

Table 3.2. Total abundance by species at JTNP and Ash Meadows Wildlife Refuge (AMWR).

	Abundance JTNP		Abundance AMWR	
Species	**Total**	**Relative (%)**	**Total**	**Relative (%)**
O. microdonta	2195	25.78	119	1.35
O. clypeata	1241	14.58	2532	28.63
O. serca	1003	11.78	37	0.42
S. difficilis	995	11.69	534	6.04
S. yumaella	866	10.17	92	1.04
S. becki	443	5.20	488	5.52
S. blakeii	436	5.12	194	2.19
O. armata	396	4.65	1	0.01
O. bellona	384	4.51	33	0.37
Dilophotopsis paron	347	4.08	47	0.53
O. inconspicua	315	3.70	567	6.41
S. mendica	256	3.01	125	1.41
O. mamata	187	2.20	303	3.43
O. delodonta	163	1.91	0	0
S. fergusoni	159	1.87	0	0
O. melicausa	133	1.56	724	8.19
O. quadrispinosa	131	1.54	4	0.05
A. dirce	129	1.52	0	0
S. amphion	118	1.39	1	0.01
S. macswaini	64	0.75	1	0.01
O. biramosa	43	0.51	3	0.03
S. angulifera	42	0.49	5	0.06
Acanthophotopsis falciformis	35	0.41	9	0.1
S. arota	31	0.36	212	2.4
S. pallidipes	27	0.32	0	0
O. sonora	14	0.16	106	1.2
S. megagnathos	14	0.16	96	1.09
O. setifera	10	0.12	7	0.08
O. dalyi, **sp. nov.**	5	0.06	0	0
O. obscura	3	0.04	0	0
S. triangularis	3	0.04	432	4.89
O. odontoloxia, **sp. nov.**	2	0.02	0	0

Table 3.2. Continued.

	Abundance JTNP		Abundance AMWR	
Species	**Total**	**Relative (%)**	**Total**	**Relative (%)**
O. parva	2	0.02	11	0.12
Photomorphus clandestine	2	0.02	0	0
S. parkeri	2	0.02	11	0.12
O. acmaea	1	0.01	130	1.47
O. aufidia	1	0.01	4	0.05
O. sublobata	1	0.01	0	0
Photomorphus schoenwerthi, **sp. nov.**	1	0.01	0	0
S. militaris	1	0.01	0	0
S. nana	1	0.01	7	0.08
Dilophotopsis concolor	0	0.00	156	1.76
O. piute	0	0.00	52	0.59
S. edwardsii	0	0.00	1	0.01
S. marpesia	0	0.00	95	1.07
S. orestes	0	0.00	1163	13.15
S. pallida	0	0.00	42	0.47
S. uro	0	0.00	397	4.49

Table 3.3. Comparison of various sites from faunal studies: Ferguson (1967), Allred (1973), Pitts *et al.* (2009, 2010a) and Boehme *et al.* (2012). Algodones = Algodones Sand Dunes (Sonoran Desert), Deep Canyon = Philip L. Boyd Deep Canyon Desert Research Center (Sonoran Desert), JTNP = Joshua Tree National Park (Sonoran and Mojave deserts), AMNWR = Ash Meadows National Wildlife Refuge (Mojave Desert) and NTS = the Nevada Test Site (Mojave Desert and Great Basin Desert). ? = may be found in this location with further collecting.

	Sonoran			Mojave		
Species	**Algodones**	**Deep Canyon**	**JTNP**	**AMNWR**	**NTS**	
Acanthophotopsis falciformis	-	-	X	?	X	X
Acrophotopsis campylognatha	-	X	-	-	-	-
Acrophotopsis dirce	-	-	X	X	X	X
Dilophotopsis concolor	-	-	-	-	X	X
Dilophotopsis paron	-	X	X	X	X	X
Odontophotopsis acmaea	X	X	?	X	X	-
O. arcuate	X	-	-	-	-	-
O. armata	-	X	X	X	X	X
O. aufidia	X	X	?	X	X	-
O. bellona	-	X	X	X	X	-
O. biramosa	X	?	X	?	X	-
O. cassia	-	-	-	-	-	X
O. clypeata	X	X	X	X	X	X
O. dalyi, **sp. nov.**	-	-	X	X	-	-
O. delodonta	-	-	X	X	-	-
O. hammetti	-	X	-	-	-	-
O. inconspicua	X	X	X	X	X	X
O. mamata	-	X	X	X	X	X
O. melicausa	X	X	X	X	X	X
O. microdonta	-	-	X	X	X	X
O. obscura	X	-	X	-	-	-
O. odontoloxia, **sp. nov.**	-	-	X	X	-	-
O. parva	-	-	X	X	X	-
O. piute	-	-	-	-	X	X
O. quadridentata	-	-	?	?	?	?
O. quadrispinosa	X	X	X	X	X	X
O. serca	-	X	X	X	X	X
O. setifera	-	X	X	?	X	X
O. sonora	X	?	X	?	X	X
O. unicornis	X	-	?	X	-	-

Table 3.3. Continued.

Species	Sonoran			Mojave		
	Algodones	Deep Canyon	JTNP		AMNWR	NTS
O. villosa	X	-	-	-	-	-
Photomorphus bicolor	X	-	-	-	-	-
Photomorphus clandestine	X	-	X	-	-	-
Photomorphus schoenwerthi, **sp. nov.**			X			
Schusterphotopsis barghesti	-	-	?	-	-	-
Sphaeropthalma amphion	-	-	X	X	X	X
S. angulifera	-	X	X	X	X	X
S. arota	X	X	X	X	X	X
S. becki	X	X	X	X	X	X
S. blakeii	X	X	X	X	X	X
S. chandleri	-	X	-	-	-	-
S. difficilis	X	X	X	X	X	X
S. django	X	-	-	-	-	-
S. ecarinata	X	-	-	-	-	-
S. edwardsii	-	-	-	-	X	-
S. fergusoni	-	X	X	X	-	-
S. ferruginea	-	X	-	-	-	X
S. ignacio	-	X	-	-	-	-
S. macswaini	X	X	X	X	X	X
S. mankelli	-	X	-	-	-	-
S. marpesia	X	-	?	?	X	-
S. meganathos	X	X	X	?	X	-
S. mendica	X	X	X	X	X	X
S. mesillensis	X	-	-	-	-	-
S. militaris	X	-	?	X	-	-
S. nana	X	-	?	X	X	X
S. orestes	-	-	?	?	X	-
S. pallida	-	X	?	?	X	X
S. pallidipes	-	-	X	-	-	-
S. parkeri	-	-	-	X	X	-
S. sublobata	-	X	X	X	-	-
S. tetracuspis	-	X	-	-	-	-
S. triangularis	X	X	X	X	X	-
S. uro	-	-	-	-	X	-
S. yumaella	X	X	X	X	X	X

other faunal studies, including the Algodones Sand Dunes, Sonoran Desert (Pitts *et al.* 2009), Philip L. Boyd Deep Canyon Desert Research Center, Sonoran Desert (Pitts *et al.* 2010), Ash Meadows National Wildlife Refuge, Mojave Desert (Boehme *et al.* 2012) and the Nevada Test Site, Mojave Desert and Great Basin Desert (Ferguson 1967; Allred 1973), are presented in Table 3.3.

***Acanthophotopsis falciformis* Schuster, 1958**

Acanthophotopsis falciformis falciformis Schuster, 1958. Ent. Amer. (n. s.) 37: 108. ♂.

Holotype data: California, Palm Springs (UMSP).

Acanthophotopsis falciformis furcisterna Schuster, 1958. Ent. Amer. (n. s.) 37: 111. ♂.

Holotype data: Arizona, Tucson (UMSP). Synonymized by Tanner *et al.* (2009).

Diagnosis of male. This species can be distinguished from other Nearctic nocturnal mutillids by the presence of a fourth mandibular tooth, which is found along the internal margin and projects posteriorly over the apex of the clypeus (see Tanner *et al.* 2009: Fig. 6). This species also has the following unique combination of characters: the dorsal carina of the mandible extends from the base of the mandible to the innermost tooth; the base of the clypeus is slightly raised, although neither carinate nor tuberculate and not horizontally produced; the frons is coarsely punctate, while the vertex moderately punctate; the length of the first flagellomere is 2 × its width; the head is strongly convergent posterior to the eyes; the length of the stigma is slightly shorter (~0.8 ×) than

the length of the marginal cell measured along the costa; the mesosternum has large conical processes; and the paramere, in lateral view, is equally broad throughout its length except for the apex, which narrows to an acute angle; and the paramere is as broad as the cuspis medially (see Pitts *et al.* 2009: Fig. 1).

Female. Unknown.

Material examined. *Acanthophotopsis falciformis falciformis* Holotype data: California, Palm Springs, fall 1932, T. Zschokke (UMSP). *Acanthophotopsis falciformis furcisterna* Holotype data: Arizona, Tucson, 5 October 1935, O. Bryant (UMSP). JTNP: 18–21.Jul.2012: 1 ♂ S13; 1 ♂ S18. 26–28.Aug.2012: 1 ♂ T. 22–24.Sep.2012: 1 ♂ T; 3 ♂ S1; 5 ♂ S5; 2 ♂ S7; 14 ♂ S9; 3 ♂ S11; 2 ♂ S13; 1 ♂ S18.

Distribution. USA (Arizona, California, and Nevada) and northern Mexico (Sonora).

Activity. This species seems to be active later in the season at JTNP.

Remarks. Pitts *et al.* (2009) illustrated the genitalia of this species and Tanner *et al.* (2009) reviewed the species in this genus and synonymized Schuster's (1958) two subspecies. Although this species is found in the Mojave Desert (e.g. Allred 1973; Boehme *et al.* 2012), this species seems to be more abundant south of the transition zone and into the Sonoran Desert (Table 3.2 & 3.3; e.g. Pitts *et al.* 2009, 2010a).

***Acrophotopsis dirce* (Fox, 1899)**

Mutilla dirce Fox, 1899. Amer. Ent. Soc., Trans. 25: 257, ♀. Holotype: Arizona, Tucson, coll. Wickham, type no. 4651 (ANSP).

Acrophotopsis eurygnathus Schuster 1958. Ent. Amer. (n. s.) 37: 11 (in key), 65, ♂. Holotype: USA, Arizona, Gila Co., Globe, 8.VII.1949, coll. Werner & Nutting (CASC). Synonymized by Pitts & Wilson (2009).

Diagnosis of male. This species is highly autapomorphic and has distinct genitalia with thick, flattened parameres that overlap *in situ* and stout cuspidis (Pitts & McHugh 2002: Figs. 12–14); the apices of the cuspis are armed with straight, stout spines and the internal border of the cuspidis are armed with short, stout, ventrally curving spines, as well as sparse setae (Pitts & McHugh 2002: Figs. l3, 14). Additionally, this species lacks mesosternal armature, but has a flattened hypopygidium that is emarginated apically and carinate laterally, and a metasoma that is darker than the head and mesosoma, or has the integument of the mesosoma at least darkened under felt lines.

Diagnosis of female. The female of *A. dirce* can be separated from that of *A. campylognatha* Schuster by the mesosoma and second metasomal tergum being only densely punctate (see Pitts & Wilson, 2009: Fig. 3) and the setae on the dorsum of the mesosoma and centrally on the second tergum being distinctly reddish-brown.

Material examined. *Mutilla dirce* Fox, Holotype: Arizona, Tucson, coll. Wickham, type no. 4651 (ANSP). *Acrophotopsis eurygnathus* Schuster Holotype: USA,

Arizona, Gila Co., Globe, 8.VII.1949, coll. Werner and Nutting (CASC). JTNP: 18–21.Jul.2012: 1 ♂ N9; 20 ♂ N7; 4 ♂ N5; 3 ♂ N3; 12 ♂ N1; 9 ♂ T; 1 ♂ S1; 1 ♂ S5; 3 ♂ S9; 1 ♂ S13; 19 ♂ S18. 26–28.Aug.2012: 6 ♂ S1; 1 ♂ S3; 6 ♂ S9; 4 ♂ S18. 22–24.Sep.2012: 1 ♂ N3; 4 ♂ S9.

Distribution. USA (Arizona, California, Nevada and Utah) and northern Mexico (Sonora).

Activity. This species seems to be active earlier in the season at JTNP.

Remarks. This genus was reviewed by Pitts & McHugh (2002), and Pitts & Wilson (2009). It is closely related to *Dilophotopsis* Schuster and *Schusterphotopsis* Pitts (Pitts 2003), with which it shares having the hypopygidium flattened and carinate posterolaterally. Although this species is found in the Mojave Desert (e.g. Ferguson 1967; Allred 1973 as *A. eurygnatha*), this species seems to be more abundant in more southern areas of the Mojave Desert and into the Sonoran Desert (Table 3.2 & 3.3).

***Dilophotopsis paron* (Cameron, 1896)**

Sphaerophthalma [sic] *paron* Cameron, 1896. Biol. Cent.-Amer. 37: 381. ♂. Syntype data: Mexico, Northern Sonora (BMNH).

Dilophotopsis concolor sonorensis Schuster, 1958. Ent. Amer. 37: 88. ♂. Holotype data: Arizona, Gila Bend (UMSP). Synonymized by Wilson & Pitts (2008).

Diagnosis of male. The male of this species has mesosternal armature, a flattened hypopygidium that is emarginated apically and carinate laterally, a metasoma that is darker than the head and mesosoma or has the integument of the mesosoma at least darkened under felt lines, and the cuspis of the genitalia is dorsoventrally flattened and uniquely elbowed (see Wilson & Pitts 2008: Figs 12–14). However, this species does not have parameres that overlap *in situ*. The mandibles are similar to *Acrophotopsis campylognatha* illustrated by Pitts *et al*. (2010a: Fig. 2).

Female Unknown.

Material examined. *Dilophotopsis concolor sonorensis* Holotype data: Arizona, Gila Bend, 24 Apr 1935, F.H. Parker (UMSP). JTNP: 18–21.Jul.2012: 49 ♂ N9; 11 ♂ N7; 41 ♂ N5; 7 ♂ N3; 5 ♂ N1; 1 ♂ S11; 2 ♂ S13; 132 ♂ S18. 26–28.Aug.2012: 1 ♂ S1; 2 ♂ S3; 1 ♂ S7; 2 ♂ S11; 2 ♂ S18. 22–24.Sep.2012: 3 ♂ S11; 3 ♂ S13.

Distribution. USA (Arizona, California, and Nevada) and northern Mexico (Baja California).

Activity. This species seems to be active earlier in the season at JTNP.

Remarks. This genus was reviewed by Wilson & Pitts (2008) and Wilson & Pitts (2010a), where they discovered that this species is morphologically and molecularly distinct from the other three subspecies, and raised it to the species level from the subspecies level. Its taxonomic position is discussed in Pitts (2003: see remarks for *Acrophotopsis dirce*). Although this species is found in the Mojave Desert (e.g. Ferguson 1967; Boehme *et al.* 2012), this species seems to be more abundant in more southern

areas of the Mojave Desert and into the Sonoran Desert (Table 3.2 & 3.3; e.g. Pitts *et al.* 2010a).

***Odontophotopsis acmaea* Viereck, 1904**

Odontophotopsis acmaeus Viereck, 1904. Amer. Ent. Soc., Trans. 30: 84. ♂. Syntype data: Arizona, (NMNH).

Odontophotopsis (*Odontophotopsis*) *grata* Schuster (nec Melander, nec Schuster 1958 p. 53, 57, 58), 1958. Ent. Amer. 37: 55. ♂. Synonymized by Pitts *et al.* (2009).

Diagnosis of male. This species has the following combination of characters: the mandible excised ventrally forming an angle, but does not taper towards the apex, the apex of the mandible is slightly dilated (see Pitts *et al.* 2010a: Fig. 3), the mesosternum has a single pair of large distinct spines that have a posterior face that is longitudinally sulcate and have an apex that is bifid, the metasternum is bidentate, and the pygidium is granulate, but not defined laterally by carinae. Genitalia are illustrated in Boehme *et al.* (2012: Fig. 2).

Female Unknown.

Material examined. Syntype data: Arizona (NMNH). USA: California: San Bernardino County: Joshua Tree National Park, Oasis of Mara, 1 ♂, 23.May.2012, (EMUS).

Distribution. USA (Arizona, California, Nevada and Utah).

Activity. This species was rare at JTNP.

Remarks. This species is in the *O. parva* species-group along with *O. aufidia, O. bellona, O. dalyi,* **sp. nov.**, *O. mamata, O. parva* and *O. odontoloxia,* **sp. nov.**, which also occur at JTNP. Although this species is found in the Sonoran and Mojave deserts (e.g. Pitts *et al.* 2009, 2010a; Boehme *et al.* 2012), this species seems to be more abundant in more northern areas of the Mojave Desert (Table 3.2 & 3.3), but not into the Great Basin Desert (e.g. Ferguson 1967).

References for genitalia illustrations are given for this species and the other *Odontophotopsis* Viereck species, but they are less diagnostic than for the other genera of nocturnal genera. Mesosternal armature and mandibular morphology are of more importance for diagnosing the species of *Odontophotopsis.*

***Odontophotopsis armata* Schuster, 1958**

Odontophotopsis (*Odontophotopsis*) *armata* Schuster, 1958. Ent. Amer. (n. s.) 37: 60. ♂.

Neotype data: California, Riverside County, Deep Canyon (EMUS).

Diagnosis of male. This species can be recognized by the presence of mesosternal processes, a deeply emarginate, tridentate mandible that is slightly oblique apically (see Boehme *et al.* 2012: Fig. 12 and Pitts *et al*. 2010a: Fig. 4), and a distinct tubercle located medially on the posterior margin of the clypeus, while usually lacking a sternal felt line.

If a sternal felt line is present, it is weak and is defined by little more than a small cluster of micropunctures. Genitalia are illustrated in Boehme *et al.* (2012; Fig. 3).

Female. Unknown.

Material examined. Neotype data: California, Riverside County, Deep Canyon, 15 males, 23–24 May 2007, Wilson, Williams and Pitts (EMUS). JTNP: 18–21.Jul.2012: 2 ♂ N7; 1 ♂ N5; 13 ♂ N1; 53 ♂ T; 38 ♂ S1; 1 ♂ S9; 3 ♂ S18. 26–28.Aug.2012: 6 ♂ N7; 1 ♂ N5; 1 ♂ N3; 8 ♂ T; 50 ♂ S1; 5 ♂ S3; 1 ♂ S5; 1 ♂ S7; 1 ♂ S13. 22–24.Sep.2012: 7 ♂ N7; 2 ♂ N3; 7 ♂ N1; 23 ♂ T; 42 ♂ S1; 1 ♂ S3; 1 ♂ S7; 1 ♂ S9.

Distribution. USA (Arizona, California, and Nevada) and northern Mexico (Baja California and Sonora).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. This species is in the *O. serca* species-group and can be sometimes confused with *O. serca*, from which it only can be separated by the presence of the clypeal tubercle, slight differences in mandibular morphology (the apex of the mandible is slightly, but noticeably, more oblique in this species) and sometimes the presence of a slight sternal felt line. This species is discussed in further detail in Pitts *et al.* (2010a).

Although this species is found in the Mojave Desert (e.g. Ferguson 1967; Boehme *et al.* 2012), this species seems to be somewhat more abundant in more southern areas of the Mojave Desert and into the Sonoran Desert (Table 3.2 & 3.3; e.g. Wilson *et al.* 2010; Pitts *et al.* 2010a).

***Odontophotopsis aufidia* Mickel, 1983 in Mickel & Clausen, 1983**

Odontophotopsis (*Odontophotopsis*) *aufidia* Mickel, 1983, in Mickel & Clausen, 1983. Ann. Amer. Ent. Soc. 76: 541. ♂. Holotype data: California, Taft (UMSP).

Diagnosis of male. This species is recognized by having the following combination of characters: the mandible is excised ventrally forming an angle and tapering towards the apex (see Pitts *et al.* 2009: Fig. 43), the mesosternum only has one pair of distinct spines, the metasternum is bidentate, and the pygidium is granulate, but is not defined laterally by carinae. Genitalia are illustrated by Pitts *et al.* (2009: Fig. 9).

Female. Unknown.

Material examined. Holotype data: California, Taft, 12 Jun 1942, W.C. Cook (UMSP). USA: California: San Bernardino County: Joshua Tree National Park, Black Rock Campground, 1 ♂, 23.Jul.2012, F. Soffel & R. Zamorano (EMUS).

Distribution. USA (Arizona, California, and Nevada).

Activity. This species was rare at JTNP.

Remarks. This species is in the *O. parva* species-group and the taxonomy of this species is discussed in further detail in Pitts *et al.* (2009). Although this species is found in the Mojave Desert (e.g. Pitts *et al.* 2009, 2010a; Boehme *et al.* 2012), this species seems to be more abundant in more southern areas of the Mojave Desert (Table 3.2 & 3.3) and Central Valley (e.g. Mickel 1983).

***Odontophotopsis bellona* Mickel, 1983 in Mickel & Clausen, 1983**

Odontophotopsis (*Odontophotopsis*) *bellona* Mickel, 1983, in Mickel & Clausen, 1983. Ann. Amer. Ent. Soc. 76: 541. ♂. Holotype data: Arizona, Pima County, Cortaro (UMSP).

Diagnosis of male. This species is differentiated by having the mandible tridentate with a large basal tooth on the ventral margin (Mickel & Clausen 1983: Fig. 17) and by the pygidium being defined laterally by carinae and having distinctly granulate sculpturing. Also this species has a mesosternal process that is bifid apically (Pitts *et al.* 2009: Fig. 106; and Mickel & Clausen 1983: Fig. 25). The genitalia are illustrated in Fig. 4 (Boehme *et al.* 2012) and by Mickel & Clausen (1983: Fig. 4).

Female. Unknown.

Material examined. Holotype data: Arizona, Pima County, Cortaro, 2100 ft, 5 Jun 1969, J. Burger (UMSP). JTNP: 18–21.Jul.2012: 4 ♂ N9; 5 ♂ N7; 8 ♂ N5; 6 ♂ N3; 2 ♂ N1; 11 ♂ T; 8 ♂ S1; 15 ♂ S3; 1 ♂ S5; 4 ♂ S7; 6 ♂ S9; 2 ♂ S11; 7 ♂ S13; 40 ♂ S18. 26–28.Aug.2012: 1 ♂ N3; 3 ♂ T; 27 ♂ S1; 45 ♂ S3; 35 ♂ S5; 6 ♂ S7; 6 ♂ S9; 6 ♂ S11; 5 ♂ S13; 3 ♂ S18. 22–24.Sep.2012: 1 ♂ N3; 6 ♂ S1; 17 ♂ S3; 4 ♂ S5; 10 ♂ S7; 33 ♂ S9; 1 ♂ S11; 3 ♂ S13; 6 ♂ S18.

Distribution. USA (Arizona, California, Nevada and Utah).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. This species is in the *O. parva* species-group and is discussed in further detail in Pitts *et al.* (2009). Although this species is found in the Mojave Desert (e.g. Boehme *et al.* 2012), this species seems to be more abundant in more southern areas of the Mojave Desert (Table 3.2 & 3.3) and into the Sonoran Desert (e.g., Mickel & Clausen, 1983; Wilson *et al.* 2010; Pitts *et al.* 2009, 2010a).

***Odontophotopsis biramosa* Schuster, 1952**

Odontophotopsis (*Odontophotopsis*) *biramosa* Schuster, 1952. Brooklyn Ent. Soc., 47: 43–47. ♂. Holotype data: California, Imperial County, Holtville (NMNH).

Odontophotopsis (*Odontophotopsis*) *biramosa* Schuster, 1958. Ent. Amer. (n. s.) 37: 56. ♂.

Diagnosis of male. This species has a tridentate mandible with an extremely large dorsal tooth that is separated from the lower portion of the mandibular apex by a deep, wide sinus, which makes the mandibular apices appear biramose (see Pitts *et al.* 2009: Fig. 29), and by the clypeus, which has a unique horseshoe-shaped tubercle posteromedially that overhangs the clypeus as a slight hood-like or nasutiform process. Also, this species has a single mesosternal process on each side of the midline, and has the cuspis being approximately half the free length of the paramere (see Pitts *et al.* 2009: Fig. 10).

Female. Unknown.

Material examined. Holotype data: California, Imperial County, Holtville, 2.Jul.1929, P.W. Owens (NMNH). JTNP: 18–21.Jul.2012: 2 ♂ S3; 4 ♂ S5; 3 ♂ S7; 1 ♂

S11; 4 ♂ S13; 1 ♂ S18. 26–28.Aug.2012: 2 ♂ S7. 22–24.Sep.2012: 3 ♂ S9; 5 ♂ S11; 6 ♂ S13. 26–28.Oct.2012: 1 ♂ S9.

Distribution. USA (Arizona, California, and Nevada).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. A more thorough taxonomic discussion of this species can be found in Pitts (2007). This species is currently placed in the *O. setifera* species-group with *O. setifera* based on mandibular morphology, but Pitts *et al.* (2010b) found these two species to not be closely related.

Although this species is found in the Mojave Desert (e.g. Boehme *et al.* 2012), this species seems to be more abundant in more southern areas of the Mojave Desert (Table 3.2 & 3.3; e.g. Wilson *et al.* 2010; Pitts *et al.* 2009, 2010a) and south of the transition zone.

***Odontophotopsis clypeata* Schuster, 1958**

Odontophotopsis (*Odontophotopsis*) *clypeata* Schuster, 1958. Ent. Amer. (n. s.) 37: 59.

♂. Holotype data: Arizona, Tucson (UMSP).

Diagnosis of male. This species has a head that is rounded posteriorly, deeply excised mandibles that are slightly dilated apically (see Boehme *et al.* 2012: Fig. 13; and Pitts *et al*. 2010a: Fig. 8), has a transverse clypeus that is slightly depressed below mandibular margins, but lacks a tubercle situated posteromedially on the clypeus, has a pair of

denticulate mesosternal processes situated anteromedially, has a shiny glabrous pygidium and has the metasoma usually castaneous, at least around the felt lines. Genitalia are illustrated by Pitts *et al.* (2009: Fig. 11).

Female. Unknown.

Material examined. Holotype data: Arizona, Tucson, 26 Aug 1939, O. Bryant (UMSP). JTNP: 18–21.Jul.2012: 1 ♂ N9; 3 ♂ N7; 2 ♂ N3; 3 ♂ N1; 1 ♂ T; 22 ♂ S1; 65 ♂ S3; 81 ♂ S5; 94 ♂ S7; 29 ♂ S9; 86 ♂ S11; 24 ♂ S13; 111 ♂ S18. 26–28.Aug.2012: 1 ♂ N7; 3 ♂ N3; 10 ♂ S1; 8 ♂ S3; 14 ♂ S5; 48 ♂ S7; 13 ♂ S9; 8 ♂ S11; 38 ♂ S13; 23 ♂ S18. 22–24.Sep.2012: 2 ♂ T; 17 ♂ S1; 55 ♂ S3; 49 ♂ S5; 61 ♂ S7; 29 ♂ S9; 14 ♂ S11; 45 ♂ S13; 76 ♂ S18. 26–28.Oct.2012: 2 ♂ S5; 20 ♂ S18.

Distribution. USA (Arizona, California, Nevada and Utah) and northern Mexico (Sonora).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. This species is widespread and common in many parts of its range and the taxonomy of this species is discussed in further detail in Pitts *et al.* (2009). It is placed in the *O. melicausa* species-group. This species is easily confused with *O. microdonta*. However, mandibular morphology and placement of the mesosternal tubercles differ (Ferguson 1967).

This species is abundant throughout its range (e.g. Pitts *et al.* 2009, 2010a). At AMWR, this species was the most abundant (e.g. Boehme *et al.* 2012). At JTNP, this species was the second most abundant species (Table 3.2 & 3.3).

***Odontophotopsis dalyi* Sadler & Pitts, sp. nov.**

Diagnosis of male. This species can be recognized by the mandibular morphology (Figs 3.1 and 3.2), especially the shape of the mandible (the mandible is vertical throughout with weak ventral tooth and slight ventral excision), the lack of mesosternal tubercles (Fig. 3.3), the well-developed sternal felt line, the dense plumose setal fringes on the apices of the metasomal segments, and the granulate pygidium that it is undefined laterally (Fig. 3.4). Genitalia are illustrated in Figs 3.13 and 3.14.

Description of male. *Coloration (Fig. 3.1).* Body testaceous; flagellum and legs stramineous; ocellular triangle piceous. Body with sparse, erect, brachyplumose, yellowish-white setae. T1 with sparse plumose fringe at distal margin. T2 and S2 with dense fringe of whitish plumose setae. T3–5 and S3–5 each with sparser, but conspicuous fringes of whitish plumose setae.

Head (Figs 3.1 and 3.2). Head slightly quadrate posteriorly. Mandible tridentate (Fig. 3.2), weakly excised beneath, excision obtuse, slight ventral tooth angulate; dorsal carina complete terminating at moderate tooth; apex vertical; mandible parallel beyond excision; mandible slightly curving ventrally towards apex. Clypeus (Fig. 3.2) depressed below margin of mandible, median area concave; surface of clypeus polished, impunctate, with few erect setae; apex truncate, not bidentate. F1 approximately 0.75 × length of F2. Ocelli (Figs 3.1 and 3.2) moderate in size, ocellocular distance approximately 1.25 × greatest width of lateral ocellus. Head weakly sculptured with punctures slightly wider than setal bases; interstitial regions glabrous.

FIGURES 3.1-3.4. *Odontophotopsis dalyi,* **sp. nov.**, 1. habitus; 2. head, frontal view; 3. mesosternum; and 4. pygidium.

Mesosoma (Fig. 3.2). Sides and dorsum of pronotum coarsely punctate, dorsum with moderate, shallow punctures, sides with somewhat larger, contiguous punctures. Mesonotum with moderate, contiguous, shallow punctures. Notaulus obsolete on anterior 0.3 of mesonotum. Scutellum coarsely, confluently punctate. Axillae not projecting posteriorly. Dorsum and posterior face of propodeum conspicuously, shallow reticulate, reticulations extending on to sides of propodeum, either remaining reticulate laterally or

becoming coarse, punctate-reticulate. Anterolateral area of mesopleuron with moderate, shallow, separated punctures; remainder of mesopleuron with deeper, contiguous to confluent punctures; interstitial areas micropunctate. Metapleuron polished. Mesosternal processes absent (Fig. 3.3), coarsely punctate. Mid and hind coxa edentate. Mid femur not swollen. Marginal cell on costa short, ~1 × length of stigma.

Metasoma (Fig. 3.1). First metasomal segment broad, nodose. Pygidium elongate and ovate, granulate along posterior margin, not margined (Fig. 3.4); S2 with felt line, 0.3 × length of tergal felt line. Hypopygidium elongate and ovate; apical margin rounded. Genitalia (Figs 3.13 and 3.14) with paramere acicular; cuspis elongate, approximately 0.5 × free length of paramere, and cylindrical in lateral view, with moderate basal pit.

Length. 10–13 mm.

Female. Unknown.

Material examined. Holotype data, ♂: USA: Arizona: *Maricopa County,* Vekol Wash, 5 km N I-8 at Vekol Rd crossing, 25.May-3.Jun.2010, M.E. Irwin & F.D. Parker (EMUS); **Paratypes:** USA: Arizona: *Maricopa County,* Vekol Wash, 5 km N I-8 at Vekol Rd crossing, 1 ♂, 25.May-3.Jun.2010, 6 ♂, 3-7.Jun.2010, M.E. Irwin & F.D. Parker (EMUS); *Yuma County*: Yuma Proving Ground, 27.Jul.2001, S.L. Buchmann (EMUS). California: *San Diego County*, Borrego, 1 ♂, 3.May.1956, P.D. Hurd (CISC). Mexico: Sonora, Desemboque, 1 ♂, 1-10.Sep.1953, B. Malkin (CISC).

Other material examined. USA: California: *Riverside County*: Joshua Tree National Park, Site S9, 2 ♂, 23-24.Sep.2012, Site N7, 1 ♂, 27.28.Aug.2012, E. Sadler & K. Weglarz (EMUS), Site S7, 2 ♂ 27-28.Oct.2012, E. Sadler & Z. Portman (EMUS).

Distribution. USA (Arizona and California).

Activity. This species was too rare at JTNP to assess its activity patterns.

Etymology. Named in honor of Carroll John Daly (1889–1958) who was a writer of crime fiction, and who has been credited with creating the first hard-boiled story and created the private detective Race Williams.

Remarks. Although this species lacks mesosternal processes, this species belongs in the *O. parva* species-group due to the head shape, mandibular morphology, bidentate metasternum, metasomal segment 1 being petiolate with segment 2 and being strongly punctate, sternal felt line, and granulate pygidium. Mesosternal processes are also lacking in *O. hammetti* Pitts, 2010*, O. rubriventris* Schuster, 1958 and *O. sonora* (Schuster). The mandibular shape is similar to that of *O. mamata*. This species could be most easily confused with *O. hammetti.* It differs, however, in the shape of the mandibles. The mandible of *O. hammetti* is straighter and is dilated apically, the hind coxae are less hirsute and the mesosternum is convex. The mandible of *O. dalyi,* **sp. nov.**, is more bent and is not dilated apically, the hind coxae are densely hirsute and the mesosternum is flattened.

***Odontophotopsis delodonta* Viereck, 1904**

Odontophotopsis delodonta Viereck, 1904. Amer. Ent. Soc., Trans. 30: 91. ♂. Holotype data: Arizona (UMSP).

Odontophotopsis (*Odontophotopsis*) *ambigua* Mickel, 1983, in Mickel & Clausen, 1983. Ann. Ent. Soc. Amer. 76: 539–541. ♂. Holotype data: California, Riverside County, Palm Springs, 8.May.1932, T. Zschokke (UMSP). **New Synonymy.**

Diagnosis of male. This species has a head that is rounded posteriorly, deeply excised mandibles that are parallel or undilated apically, lacks a tubercle situated posteromedially on the clypeus, has a pair of denticulate mesosternal processes that are small and indistinct, the integument is orange even beneath the felt lines, and has a shiny glabrous pygidium.

Additions to Viereck's description of male. Integument orangish. Mandible excised beneath, ~0.6 × basal width, not dilated apically. Clypeal base not tuberculate, convex. Apical margin slightly emarginated. Antenna stramineous. Ocellular area slightly infuscated. OOD ~1.5 and IOD ~1.25 lateral ocellus. Legs stramineous. Mesopleura anteriorly glabrous with few large punctures, with few plumose setae. Mesosternal processes single pair, small, indistinct, approximate. Dense plumose setae posterior to processes. MC slightly longer than stigma, ~1.2 × stigma. MC rounded apically. T1 shallow punctures laterally, glabrous medially, with plumose fringe. T2–T6 with plumose fringes. Pygidium weakly granulate with apical fringe of setae. S2 slightly tumid mediobasally. Hypopygidium punctate throughout, rounded apically.

Female. Unknown.

Material examined. Holotype data: Arizona (UMSP). Holotype data: California, Riverside County, Palm Springs, 8.May.1932, T. Zschokke (UMSP). JTNP: 18–

21.Jul.2012: 1 ♂ N3; 1 ♂ T; 1 ♂ S1; 5 ♂ S3; 1 ♂ S9; 1 ♂ S11. 26–28.Aug.2012: 1 ♂ N7; 4 ♂ S1; 1 ♂ S3; 4 ♂ S5; 45 ♂ S7; 36 ♂ S9; 8 ♂ S11; 3 ♂ S13; 1 ♂ S18. 22–24.Sep.2012: 1 ♂ N7; 1 ♂ S1; 1 ♂ S3; 4 ♂ S5; 7 ♂ S7; 11 ♂ S9; 9 ♂ S11; 14 ♂ S13.

Distribution. USA (Arizona, California, and Nevada).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. Viereck's original description stated that the antennae and legs were pale testaceous. The holotype, however, has the legs and antennae stramineous. Study of the holotype and paratypes of, as well as variation in, *O. ambigua* revealed that the characters Mickel (in Mickel & Clausen, 1983) used to separate *O. delodonta* and *O. ambigua*, namely presence or absence of an indistinct clypeal tubercle, are not significant. As such these species are considered conspecific here. This species is a member of the *O. melicausa* species-group.

Although this species is found in the Mojave Desert, this species seems to be more abundant in more southern areas of the Mojave Desert (Table 3.2 & 3.3) and into the Sonoran Desert, as it was not found at the NTS (e.g. Ferguson 1967) or AMWR (e.g. Boehme *et al.* 2012).

***Odontophotopsis inconspicua* (Blake, 1886)**

Photopsis inconspicuus Blake, 1886. Amer. Ent. Soc., Trans. 13: 272. ♂. Holotype data: California (ANSP).

Mutilla infelix Dalla Torre, 1897. Cat. Hym. 50. New name for *Photopsis inconspicuous* Blake not *Mutilla inconspicuus* Smith.

Diagnosis of male. This species has the following combination of characters: the mandible is excised ventrally, forming a slight tooth that is dilated towards the apex (see Pitts *et al.* 2009: Fig. 32), the mesosternum only has one pair of large distinct spines that are flattened to slightly concave on the posterior side, the metasternum is tridentate, the second sternum of the metasoma lacks a felt line, and the pygidium is granulate and is defined laterally by carinae. Genitalia are illustrated by Pitts *et al.* (2009: Fig. 12).

Diagnosis of female. The female of this species can be diagnosed by dense appressed setae present on the dorsum that obscures the integumental sculpture and are distinctly plumose at the base of the setal shaft becoming simple apically. Also the ventral margin of the mandible has a distinct angulation, flagellomere 1 is much longer than flagellomere 2, the mesosoma is hexagonal in dorsal view, the first segment of the metasoma is sessile with the second, and the second metasomal segment is of normal length being ~1 × as long as anterior width or just slightly greater.

Material examined. Holotype data: California (ANSP). JTNP: 18–21.Jul.2012: 1 ♂ N1; 5 ♂ T; 2 ♂ S1; 1 ♂ S3; 1 ♂ S11; 36 ♂ S18. 26–28.Aug.2012: 3 ♂ N3; 3 ♂ N1; 11 ♂ T; 102 ♂ S1; 11 ♂ S3; 1 ♂ S5; 3 ♂ S7; 23 ♂ S9; 5 ♂ S11; 11 ♂ S13; 19 ♂ S18. 22–24.Sep.2012: 1 ♂ N7; 2 ♂ N3; 1 ♂ N1; 1 ♂ T; 6 ♂ S3; 2 ♂ S5; 3 ♂ S7; 23 ♂ S9; 5 ♂ S11; 11 ♂ S13; 19 ♂ S18. 26–28.Oct.2012: 1 ♂ S3; 4 ♂ S9.

Distribution. USA (Arizona, California, Nevada and Utah).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. Pitts *et al.* (2009) recently associated the sexes using distributional and morphological data. Further taxonomic description of this species can also be found in Pitts *et al.* (2009). This species is a member of the *O. venusta* species-group and is seemingly abundant throughout its range (Table 3.2 & 3.3; e.g. Wilson *et al.* 2010; Pitts *et al.* 2009, 2010a; Boehme *et al.* 2012).

***Odontophotopsis mamata* Schuster, 1958**

Odontophotopsis (*Periphotopsis*) *mamata* Schuster, 1958. Ent. Amer. (n. s.) 37: 60. ♂.

Holotype data: Arizona, Ehrenberg (UMSP).

Diagnosis of male. This species can be easily recognized by the distinct mesosternal processes, which are made up of large glabrous longitudinal swellings located on either side of the midline. Genitalia are illustrated in Boehme *et al.* (2012: Fig. 5) with the paramere having a characteristic bend at approximately 0.66 × the free length from the base, and the mandibles can be viewed in Pitts *et al*. (2010a: Fig. 10).

Female. Unknown.

Material examined. Holotype data: Arizona, Ehrenberg, 12 June 1935, F.H. Parker (UMSP). JTNP: 18–21.Jul.2012: 12 ♂ T; 18 ♂ S1; 3 ♂ S3; 2 ♂ S7; 1 ♂ S9; 7 ♂ S18. 26–28.Aug.2012: 10 ♂ T; 34 ♂ S1; 11 ♂ S3; 1 ♂ S5; 4 ♂ S7; 3 ♂ S18. 22–

24.Sep.2012: 1 ♂ N1; 7 ♂ T; 23 ♂ S1; 5 ♂ S3; 1 ♂ S5; 2 ♂ S9; 4 ♂ S11; 2 ♂ S13; 2 ♂ S18. 26–28.Oct.2012: 2 ♂ S18.

Distribution. USA (Arizona, California, Nevada and Utah).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. This species is placed in the *O. parva* species-group and the taxonomy of this species is discussed in further detail in Pitts *et al.* (2009). This species is abundant throughout its range (Table 3.2 & 3.3; e.g. Boehme *et al.* 2012), but for this study was more abundant at and south of the transition zone. It is a common species in the Sonoran Desert (e.g. Wilson *et al.* 2010; Pitts *et al.* 2010a).

***Odontophotopsis melicausa* (Blake, 1871)**

Agama melicausa Blake, 1871. Amer. Ent. Soc., Trans. 3: 261. ♂. Holotype data: Texas (ANSP).

Mutilla brevicornis Fox, 1899. Amer. Ent. Soc., Trans. 25: 255. ♂. Syntype data: Texas; Montana (ANSP). Synonymized by Schuster (1958).

Odontophotopsis mellicornis Baker, 1905. Invertebrata Pacifica 1: 96. ♂. Holotype data: Nevada, Ormsby County, (CUIC). Synonymized by Schuster (1958).

Diagnosis of male. This species has a head that is quadrate posteriorly, deeply excised mandibles that are distinctly dilated apically (see Pitts *et al.* 2009: Fig. 33), lacks a tubercle situated posteromedially on the clypeus, has a pair of denticulate mesosternal

processes, and has a shiny glabrous pygidium. Genitalia are illustrated by Pitts *et al.* (2009: Fig. 13).

Female. The female of this species has dense appressed setae on the dorsum that obscures the integumental sculpture and are distinctly plumose at the base of the setal shaft becoming simple apically. Also the ventral margin of the mandible is excised and has a rounded tooth, flagellomere 1 is longer than flagellomere 2, the lateral margins of the posterior half of the mesosoma are parallel in dorsal view, the first segment of the metasoma is petiolate with the second, the second metasomal segment is of normal length being ~1 × as long as anterior width or just slightly greater, and the pygidium is strongly striate.

Material examined. *Agama melicausa* Holotype data: Texas, Belfrage (ANSP). *Mutilla brevicornis* Syntype data: Texas; Montana (ANSP). *Odontophotopsis mellicornis* Holotype data: Nevada, Ormsby County, (CUIC). JTNP: 18–21.Jul.2012: 7 ♂ N9; 9 ♂ N7; 1 ♂ S1; 3 ♂ S11; 2 ♂ S13; 16 ♂ S18. 26–28.Aug.2012: 3 ♂ N7; 5 ♂ N3; 2 ♂ T; 3 ♂ S1; 1 ♂ S7; 2 ♂ S11; 3 ♂ S13. 22–24.Sep.2012: 3 ♂ N9; 3 ♂ N7; 4 ♂ N3; 4 ♂ S11; 8 ♂ S13; 7 ♂ S18.

Distribution. USA (Arkansas, Arizona, California, Colorado, Idaho, Kansas, Montana, Nevada, New Mexico, Oklahoma, Oregon, Texas, Utah, Washington, and Wyoming), Canada (British Columbia) and northern Mexico (Baja California, Chihuahua, and Sonora).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. The taxonomy of this species is discussed in further detail in Pitts *et al.* (2009). Although this species is found throughout the west (e.g. Wilson *et al.* 2010; Pitts *et al.* 2009, 2010a; Boehme *et al.* 2012), this species seems to be more abundant in more northern areas of the Mojave Desert (Table 3.2 & 3.3) and into the Great Basin Desert. This species is a member of the *O. melicausa* species-group.

***Odontophotopsis microdonta* Ferguson, 1967**

Odontophotopsis (Odontophotopsis) microdonta Ferguson, 1967. Brigham Young Univ. Sci., Bul., Ser. 8, no. 4: 22. ♂. Holotype data: Nevada, Nye County, 5 mi. NNW Mercury (NMNH).

Diagnosis of male. This species has a head that is rounded posteriorly, deeply excised mandibles that are slightly dilated apically (see Boehme *et al.* 2012: Fig. 14), has a transverse clypeus that is slightly depressed below mandibular margins, but lacks a tubercle situated posteromedially on the clypeus, has a pair of denticulate mesosternal processes situated more laterally and posteriorly than in *O. clypeata*, has a shiny glabrous pygidium and the metasoma is usually castaneous, at least around the felt lines. Genitalia are illustrated in Boehme *et al.* (2012: Fig. 6).

Female. Unknown.

Material examined. Holotype data: Nevada, Nye County, 5 mi. NNW Mercury, 25 Aug 1964, W. E. Ferguson (NMNH). JTNP: 18–21.Jul.2012: 64 ♂ N9; 22 ♂ N7; 62 ♂ N5; 41 ♂ N3; 10 ♂ N1; 16 ♂ T; 3 ♂ S1; 49 ♂ S3; 8 ♂ S5; 2 ♂ S7; 31 ♂ S9; 536 ♂ S11;

79 ♂ S13; 29 ♂ S18. 26–28.Aug.2012: 7 ♂ N9; 21 ♂ N7; 2 ♂ N5; 67 ♂ N3; 1 ♂ N1; 3 ♂ S1; 4 ♂ S3; 1 ♂ S5; 2 ♂ S7; 1 ♂ S9; 23 ♂ S11; 50 ♂ S13; 14 ♂ S18. 22–24.Sep.2012: 8 ♂ N9; 10 ♂ N7; 10 ♂ N5; 17 ♂ N3; 11 ♂ N1; 3 ♂ T; 7 ♂ S1; 142 ♂ S3; 14 ♂ S5; 7 ♂ S7; 10 ♂ S9; 154 ♂ S11; 157 ♂ S13; 91 ♂ S18. 26–28.Oct.2012: 1 ♂ S9; 1 ♂ S11.

Distribution. USA (Arizona, California, and Nevada).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. This species was first described by Ferguson (1967) from the NTS and is most abundant in the Mojave Desert (e.g. Wilson *et al.* 2010; Boehme *et al.* 2012). At JTNP, this species was the most abundant species (Table 3.2 & 3.3). This species is a member of the *O. melicausa* species-group.

***Odontophotopsis obscura* Schuster, 1958**

Odontophotopsis (*Odontophotopsis*) *territa obscura* Schuster, 1958. Ent. Amer. (n. s.) 37: 59. ♂. Neotype data: California, Imperial County, 3 mi NW Glamis, 15–16.Sep.1972, M.S. Wasbauer and A. Hardy (CDFA).

Diagnosis of male. This species has a head that is rounded posteriorly, has deeply excised mandibles that are slightly dilated apically, lacks a tubercle situated posteromedially on the clypeus, and has an elongate clypeus that is level with the mandibular margins, has a pair of denticulate mesosternal processes, and has a shiny glabrous pygidium. The genitalia are illustrated in Pitts *et al.* (2009: Figs. 14 and 15).

Diagnosis of female. The female of this species has the ventral margin of the mandible being excised and having a rounded tooth (Pitts *et al.* 2009: Fig. 34), flagellomere 1 being as long as flagellomere 2, the lateral margins of the posterior half of the mesosoma being parallel in dorsal view, the first segment of the metasoma being petiolate with the second, the second metasomal segment being of normal length, ~1 × as long as anterior width or just slightly greater, the pygidium being weakly striate to granulate, and by the dense appressed setae present on the dorsum that obscure the integumental sculpture and are distinctly plumose at the base of the setal shaft becoming simple apically.

Material examined. Neotype data: California, Imperial County, 3 mi NW Glamis, 15–16.Sep.1972, M.S. Wasbauer and A. Hardy (CDFA). JTNP: 18–21.Jul.2012: 2 ♂ S9. 22–24.Sep.2012: 1 ♂ S9.

Distribution. USA (Arizona and California).

Activity. This species is seemingly rare at JTNP.

Remarks. This species is placed in the *O. melicausa* species-group and is likely sister to *O. territa* Schuster, 1958 (Pitts *et al.* 2009). This species is most abundant in the Sonoran Desert (e.g. Wilson *et al.* 2010; Pitts *et al.* 2009, 2010a).

***Odontophotopsis odontoloxia* Sadler & Pitts, sp. nov.**

Diagnosis of male. This species can be immediately recognized by the mandibular morphology alone, where the third (dorsal) tooth at the apex of the mandible is dilated

dorsally (Fig. 3.6). This is a unique mandibular shape for nocturnal mutillids. Also, the prominent mesosternal tubercles (Fig. 3.7), the well-developed sternal felt line, the dense plumose setal fringes on the apices of the metasomal segments, and the granulate pygidium (Fig. 3.8) that it is defined laterally delimit this species. Genitalia are illustrated in Figs 3.15 and 3.16.

Description of male. *Coloration (Fig. 3.5).* Body testaceous; antenna and legs stramineous; ocellular triangle infuscated. Body clothed with sparse, erect, brachyplumose, yellowish-white setae. T1, T2 and S2 with sparse fringe of whitish plumose setae. T3–5 and S3–5 each with sparser, but conspicuous fringes of whitish plumose setae.

Head (Fig. 3.6). Head rounded posteriorly. Mandible (Fig. 3.6) tridentate, weakly but broadly excised beneath, excision obtuse, ventral tooth small, angulate; dorsal carina complete terminating at large tooth with angulate dorsal lamella; apex vertical; mandible dilated beyond excision; mandible slightly curving ventrally towards apex. Clypeus (Fig. 3.6) depressed below margin of mandible, median area concave; surface of clypeus polished, impunctate, with few erect setae; apex truncate, not bidentate. F1 approximately 0.8 × length of F2. Ocelli (Figs 3.5 and 3.6) moderate in size, ocellocular distance approximately 2 × greatest width of lateral ocellus. Head weakly sculptured with punctures slightly wider than setal bases; interstitial regions glabrous.

Mesosoma (Fig. 3.5). Sides and dorsum of pronotum coarsely punctate, dorsum with moderate, shallow punctures, sides with somewhat larger, contiguous punctures. Mesonotum with moderate, contiguous, shallow punctures. Notaulus obsolete on anterior

FIGURES 3.5-3.8. *Odontophotopsis odontoloxia,* **sp. nov.**, 5. habitus; 6. head, frontal view; 7. mesosternum; and 8. pygidium.

0.3 of mesonotum. Scutellum coarsely, confluently punctate. Axillae not projecting posteriorly. Dorsum and posterior face of propodeum conspicuously, shallow reticulate, reticulations extending on to sides of propodeum, either remaining reticulate laterally or becoming coarse, punctate-reticulate. Anterolateral area of mesopleuron with moderate, shallow, separated punctures; remainder of mesopleuron with deeper, contiguous to confluent punctures; interstitial areas micropunctate. Metapleuron polished. Mesosternum (Fig. 3.7) bidentate, tubercles large, triangular and concave in posterior view; sinus

between tubercles U-shaped. Mid and hind coxa edentate. Mid femur not swollen. Marginal cell on costa short, ~1 × length of stigma.

Metasoma (Fig. 3.5). First metasomal segment broad, nodose. Pygidium (Fig. 3.8) elongate and ovate, distinctly granulate along posterior margin, strongly margined laterally; S2 with felt line, 0.3 × length of tergal felt line. Hypopygidium elongate and ovate; apical margin rounded. Genitalia (Figs 3.15 and 3.16) with paramere acicular; cuspis elongate, approximately 0.5 × free length of paramere, and cylindrical in lateral view, with moderate basal pit.

Length. 10–13 mm.

Female. Unknown.

Material examined. Holotype data, ♂: USA, Nevada, *Clark County*, St. Thomas Gap, 1 ♂, 27.Aug.1998, C. Shultz, O. & S. Messinger (CISC). **Paratype:** USA, *Riverside County*, Wileys Well, 1 ♂, 6.Oct.1988, T. Griswold (EMUS).

Other material examined. USA: California: *San Bernardino County*: Joshua Tree National Park, Dale Mine, 1 ♂, 25.Jun.2012, F. & J. Cambon (EMUS); *Riverside County*, Fig 8, 3.15-3.18 Joshua Tree National Park, Site S5, ♂, 22-23.Sep.2012, E. Sadler & K. Weglarz (EMUS).

Distribution. USA (California, and Nevada).

Activity. This species is rare and we were unable to assess activity patterns.

Etymology. From the Greek *odonto*- meaning tooth and the Greek *–loxos* meaning slanting. *Odontoloxia* is a common dental term for irregular teeth made in reference to the snaggletoothed appearance of this species' mandible.

Remarks. This species belongs in the *O. parva* species-group due to the head shape, mandibular morphology, bidentate metasternum, metasomal segment 1 being petiolate with segment 2 and being strongly punctate, sternal felt line, and defined granulate pygidium. The mesosternal processes are similar to *O. parva* and *O. acmaea*, and specimens of this species may be misidentified as *O. acmaea* in collections.

***Odontophotopsis parva* Schuster, 1958**

Odontophotopsis (Odontophotopsis) parva Schuster, 1958. Ent. Amer. (n. s.) 37: 55. ♂.

Holotype data: Arizona, Arlington (UMSP).

Diagnosis of male. This species has the mandible excised ventrally forming an angle, but does not taper towards the apex (see Pitts *et al.* 2009: Fig. 35), the mesosternum has only one pair of large distinct spines that have a posterior face that is longitudinally sulcate, the metasternum is bidentate, and the pygidium is granulate and is defined laterally by carinae. The genitalia are illustrated by Pitts *et al.* (2009: Figs 16, 17).

Diagnosis of female. The female of this species has the ventral margin of the mandible having a distinct angulation (see Pitts *et al.* 2009: Fig. 35), flagellomere 1 being only slightly longer than flagellomere 2, the lateral margins of the posterior half of the mesosoma being parallel in dorsal view, the first segment of the metasoma being sessile with the second, the second metasomal segment being of normal length, ~1 × as long as anterior width or just slightly greater, the pygidium being longitudinally striate, and by

the dense appressed setae present on the dorsum that obscure the integumental sculpture and are distinctly plumose at the base of the setal shaft becoming simple apically.

Material examined. Holotype data: Arizona, Arlington, 17.Jun.1919, A. Wetmore (UMSP). JTNP: 26–28.Aug.2012: 2 #m S9. USA: California: San Bernardino County: Joshua Tree National Park, Dale Mine, 1 ♂, 25.Jun.2012, F. & J. Cambon (EMUS).

Distribution. USA (Arizona, California, and Nevada) and northern Mexico (Sonora).

Activity. This species is seemingly rare at JTNP.

Remarks. This species is in the *O. parva* species-group and the taxonomy of this species has been discussed in Pitts *et al.* (2009). This species seems to be rare throughout its range (Table 3.2 & 3.3; e.g. Pitts *et al.* 2009).

Odontophotopsis quadridentata Schuster, 1958

Odontophotopsis (*Odontophotopsis*) *quadridentata* Schuster, 1958. Ent. Amer. (n. s.) 37: 51, ♂. Holotype: California, Kern Co., Taft, 13.Jun.1942, W.C. Cook (UMSP).

Diagnosis of male. This species has unique mesosternal processes. The mesosternum is armed along the midline with four separated subequal spine-like processes, with two processes on each side of midline that are arranged in almost a square shaped pattern with the posterior pair slightly wider apart than the anterior pair. Sometimes a third smaller

tooth is present posterior to the second tooth as in Fig. 24 (in Pitts 2007). The setal coloration varies from white to pale golden, while the integument is orange. The mandible is tridentate and deeply excised ventrally (see Pitts 2007: Fig. 23) with the apical portion moderately dilated, but not contorted or ventrally curved as in *O. exogyra* (see Pitts 2007: Fig. 13, 14). Also, the metasoma is petiolate and slightly nodose, the pygidium varies from polished to slightly granulate but is undefined laterally and has a dense apical fringe of setae.

Material examined. Holotype: California, Kern Co., Taft, 13.Jun.1942, W.C. Cook (UMSP).

Distribution. USA (Arizona, California, Nevada and Utah).

Remarks. This species was not collected in the course of this study and specimens have not been seen of it from JTNP, but may occur in JTNP. This species was reviewed in Pitts (2007) and is placed in its own species-group.

***Odontophotopsis quadrispinosa* Schuster, 1958**

Odontophotopsis quadrispinosa Schuster, 1958. Ent. Amer. 37: 51. ♂. Neotype data: California, Palm Springs (UMSP).

Diagnosis of male. This species can be recognized by having the marginal cell much shorter than the stigma as measured along the costal vein, and two pairs of mesosternal processes forming a square, with the anterior pair much more obvious than the posterior

pair. Also, the mandibles are deeply emarginate along the ventral margin, but the mandible narrows towards the apex (see Pitts 2007: Fig. 67). Genitalia are illustrated by Pitts *et al.* (2009: Fig. 18).

Female. Unknown.

Material examined. Neotype data: California, Palm Springs, 1 May 1933, At light, Theo. Zschokke (UMSP). JTNP: 18–21.Jul.2012: 2 ♂ T; 6 ♂ S3; 1 ♂ S11; 2 ♂ S18. 26–28.Aug.2012: 2 ♂ N3; 7 ♂ S1; 9 ♂ S3; 5 ♂ S5; 10 ♂ S7; 9 ♂ S9; 12 ♂ S11; 4 ♂ S13; 1 ♂ S18. 22–24.Sep.2012: 1 ♂ N3; 11 ♂ S3; 6 ♂ S5; 10 ♂ S7; 17 ♂ S9; 11 ♂ S11; 2 ♂ S18.

Distribution. USA (Arizona, California, and Nevada) and northern Mexico (Baja California and Sonora).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. This species is rare throughout its range and the taxonomy of this species is discussed in Pitts *et al.* (2009). This species can be difficult to identify, because the mesosternal processes are weak and sometimes difficult to observe. As such, this species could be confused as a species of *Sphaeropthalma*, but the genitalia are distinct. This species is typically rare throughout its range, but seems to be locally abundant at times (Table 3.2 & 3.3; e.g. Pitts *et al.* 2009, 2010a) and was collected in this study south of the transition zone. This species is placed in its own species-group.

***Odontophotopsis serca* Viereck, 1904**

Odontophotopsis sercus Viereck, 1904. Amer. Ent. Soc., Trans 30: 87. ♂. Holotype data: Mexico, Lower California (ANSP).

Diagnosis of male. This species can be recognized by the lack of a clypeal tubercle, by having deeply excised mandibles with a vertical apex (see Boehme *et al.* 2012: Fig. 8), by having simple but prominent mesosternal processes, and by lacking a sternal felt line. Genitalia are illustrated in Boehme *et al.* (2012: Fig. 16).

Female. Unknown.

Material examined. Holotype data: Mexico, Lower California, type no. 4979 (ANSP).

JTNP: 18–21.Jul.2012: 3 ♂ N9; 1 ♂ N7; 1 ♂ N5; 3 ♂ N3; 19 ♂ N1; 123 ♂ T; 107 ♂ S1; 9 ♂ S3; 4 ♂ S5; 2 ♂ S9; 6 ♂ S11; 3 ♂ S13; 15 ♂ S18. 26–28.Aug.2012: 3 ♂ N7; 2 ♂ N3; 24 ♂ N1; 130 ♂ T; 187 ♂ S1; 9 ♂ S3; 1 ♂ S5; 2 ♂ S7; 3 ♂ S9; 8 ♂ S11; 3 ♂ S13; 1 ♂ S18. 22–24.Sep.2012: 2 ♂ N7; 3 ♂ N3; 8 ♂ N1; 3 ♂ T; 81 ♂ S1; 1 ♂ S3; 5 ♂ S9; 3 ♂ S11; 1 ♂ S18.

Distribution. USA (Arizona, California, and Nevada) and northern Mexico (Baja California and Sonora).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. *Odontophotopsis serca,* unlike *O. armata,* never develops a felt line on the second metasomal sternum, but can be easily confused with this species. The clypeal tubercle, however, is distinct in *O. armata.* This species is a member of the *O. serca* species-group along with *O. armata* and *O. mariae* (Cameron, 1896). This species, along with *O. melicausa,* sometimes develops a slight secondary mesosternal tubercle posterior to the primary one and is sometimes unilateral (Ferguson 1967). The taxonomy of this species is discussed in more detail in Pitts *et al.* (2009). Although this species is found in the Mojave Desert (e.g. Ferguson 1967; Boehme *et al.* 2012), this species seems to be more abundant in more southern areas of the Mojave Desert and into the Sonoran Desert (Table 3.2 & 3.3; e.g. Wilson *et al.* 2010; Pitts *et al.* 2010a).

***Odontophotopsis setifera* Schuster, 1952**

Odontophotopsis (*Odontophotopsis*) *setifera* Schuster, 1952. Brooklyn Ent. Soc., 47: 47–49, ♂. Holotype data: California, Riverside County, Palms to Pines Highway (UMSP).

Odontophotopsis (*Odontophotopsis*) *setifera* Schuster, 1958. Ent. Amer. (n. s.) 37: 56, ♂.

Diagnosis of male. This species can be recognized by its unique mandibular morphology. The mandible has the apex vertical and has four teeth with the dorsal tooth is separated from the remaining teeth by a deep sinus (see Boehme *et al.* 2012: Fig. 17). Other

potentially useful characters are listed in Pitts (2007) and Pitts *et al.* (2009). Genitalia are illustrated by Pitts (2007: Figs 30, 31).

Female. Unknown.

Material examined. Holotype data: California, Riverside County, Palms to Pines Highway, 28 May 1940, R.M. Bohart (UMSP). JTNP: 18–21.Jul.2012: 8 ♂ S18.

Distribution. USA (Arizona, California, Nevada and Utah) and northern Mexico (Baja California).

Activity. This species is seemingly rare at JTNP.

Remarks. A more thorough taxonomic discussion of this species can be found in Pitts (2007). This species is currently placed in the *O. setifera* species-group with *O. biramosa* (see discussion for this species). This species is seemingly rare throughout its range (Table 3.2 & 3.3; e.g. Ferguson 1967; Pitts 2007; Wilson *et al.* 2010; Pitts *et al.* 2010a; Boehme *et al.* 2012).

***Odontophotopsis sonora* Schuster, 1958**

Sphaeropthalma (*Micromutilla*) *sonora* Schuster, 1958. Ent. Amer. 37: 16. ♂. Holotype data: Arizona, Tucson (UMSP).

Diagnosis of male. This species can be recognized by the lack of a tooth on the ventral margin of the mandible, the mandibular apex is tridentate and oblique (see Pitts 2007: Fig. 32), and by the clypeus being elongate and projecting over the dorsal margins of the

mandibles. Also, this species lacks mesosternal armature, even though it is placed in the genus *Odontophotopsis*. Genitalia are illustrated by Pitts *et al.* (2009: Figs 20, 21).

Female. Unknown, but will possibly be similar to the females of the *O. melicausa* species-group based on male morphology.

Material examined. Holotype data: Arizona, Tucson, 10 Sep 1935. Bryant (UMSP). JTNP: 26–28.Aug.2012: 1 ♂ S3; 4 ♂ S7; 4 ♂ S9. 22–24.Sep.2012: 1 ♂ S1; 1 ♂ S5; 1 ♂ S7.

Distribution. USA (Arizona, California, and Nevada).

Activity. This species is seemingly rare at JTNP.

Remarks. Pitts (2007) moved this species from *Sphaeropthalma* to *Odontophotopsis* based on genitalic morphology and presence of dense plumose fringes on the metasoma, even though the species lacks mesosternal tubercles. Pitts *et al.* (2010b) performed a molecular phylogenetic analysis and confirmed this taxonomic change. It is placed in its own species-group. Although this species is found in multiple deserts (e.g. Ferguson 1967; Pitts 2007; Pitts *et al.* 2009; Boehme *et al.* 2012), this species seems to be more abundant in the more northern areas of its range in the Mojave Desert (Table 3.2 & 3.3).

***Odontophotopsis unicornis* Schuster, 1958**

Odontophotopsis (*Odontophotopsis*) *unicornis* Schuster, 1958. Ent. Amer. (n. s.) 37: 52.

♂. Neotype data: USA: AZ: Graham Co., 2.4 mi W Hwy 366 From Hwy 191, 3800', 14–26.Aug.1993, Hara (EMUS).

Diagnosis of male. This species has the clypeus concave with a tuberculate process at median proximal margin, but the process is narrowly linguiform, is produced downward over clypeus, is prominent and is much longer than wide (see Pitts *et al.* 2009: Fig. 108). Additionally, the anterior margin of the clypeus is distinctly emarginated and turned outward, the ocellar area usually is concolorous with the head, but sometimes slightly infuscated, the cuspis is slightly narrowed medially having an apex with stout setae while having thinner setae medially and has an inner margin with circular area of dense short setae. Genitalia are as in Pitts (2007: Figs. 54–56).

Female. Unknown.

Material examined. Neotype data: USA: AZ: Graham Co., 2.4 mi W Hwy 366 From Hwy 191, 3800', 14–26.Aug.1993, Hara (EMUS). USA: California: San Bernardino County: Joshua Tree National Park, Oasis of Mara, 1 ♂, 20.Sep.2012, D. Garrett (EMUS).

Distribution. USA (Arizona, California, and Nevada) and northern Mexico (Baja California and Sonora).

Activity. This species is seemingly rare at JTNP.

Remarks. Pitts (2007) was unable to locate Schuster's holotype for this species and designated a Neotype. A more thorough discussion of this species can be found in

Pitts (2007) and Wilson & Pitts (2010b). This species is most common in the Sonoran Desert (e.g. Pitts *et al.* 2009; Wilson *et al.* 2010) and is in the *O. unicornis* species-group along with *O. erebus* (Melander, 1903).

***Photomorphus clandestina* (Viereck), 1903**

Odontophotopsis clandestinus Viereck, 1903. Acad. Nat. Sci. Phila., Proc. 54: 740. ♂.

Holotype data: New Mexico, Mesilla, July 31, T.D.A. Cockerell (ANSP).

Diagnosis of male. This species is recognized by the mesosternum bearing tubercles that have apical transverse grooves, by the mesoscutum with pale white setae, by the apex of the fore wings usually without maculations, by the granulate pygidium, by the penal valve of the genitalia being hidden from view laterally by the parapenial lobes and by the cuspis being ~0.5× the free length of the paramere.

Diagnosis of female. Unknown.

Material examined. Holotype data: USA: New Mexico, Mesilla, July 31, T.D.A. Cockerell (ANSP). JTNP: 18–21.Jul.2012: 2 ♂ S13.

Distribution. USA (Arizona, California, and New Mexico) and northern Mexico (Sonora).

Activity. This species was too rare at JTNP to assess its activity patterns.

***Photomorphus schoenwerthi* Sadler & Pitts, sp. nov.**

Diagnosis of male. This species is recognized by the mesosternum (Fig. 3.11) bearing tubercles that have apical transverse grooves, by the morphology of the mandible (Fig. 3.10), by the mesoscutum with golden setae (Fig. 3.9), by the apex of the fore wings with maculations, by the granulate pygidium (Fig. 3.12), by the penal valve of the genitalia being hidden from view laterally by the parapenial lobes and by the cuspis being ~0.66× the free length of the paramere (Figs 3.17 and 3.18).

Description of male. *Coloration (Fig. 3.9).* Body ferruginous, except antennae slightly infuscated. Pubescence of body pale, except mesoscutum and T5-7 golden yellow. Ocellar area concolorous with head. Wings hyaline, maculation present posterior to stigma.

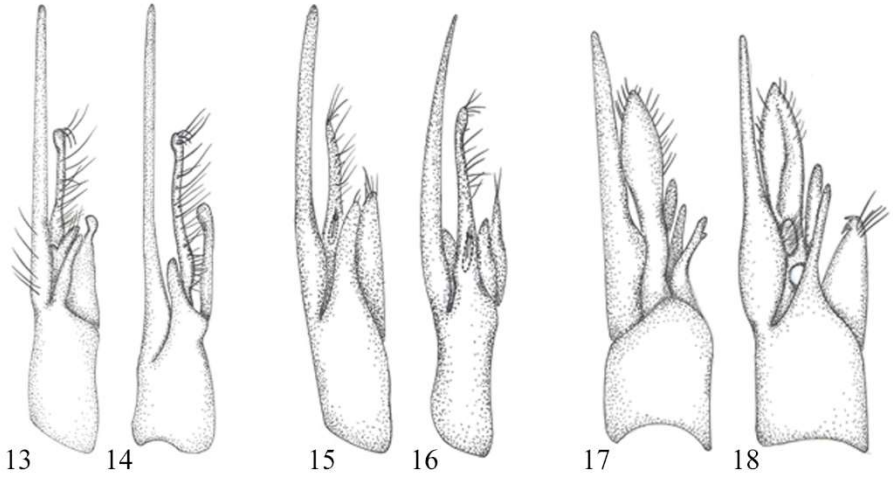
Head (Fig. 3.10). Mentum carinulate. Head quadrate posteriorly. Mandible (Fig. 3.10) tridentate, deeply excised ventrally, slightly constricted at excision and slightly dilated beyond excision. Clypeus depressed below margin of mandible, median area concave; surface of clypeus polished, impunctate, with few erect setae; apex truncate, proximal margin of clypeus weakly to moderately tuberculate. Front, vertex and gena closely punctate; those on front more closely punctate than those on gena and vertex. Ocelli moderate in size, ocellocular distance 1.7 × length of lateral ocellus. F1 approximately 0.75 × length of F2.

Mesosoma (Fig. 3.9). Pronotum coarsely punctured, punctures contiguous to confluent. Mesonotum coarsely punctured, punctures slightly separated on disk, dense

and confluent laterally. Anterior half of parapsidial furrows and notauli absent. Axillae slightly projecting posteriorly as small rounded structures. Scutellum densely punctured. Dorsum and posterior face of propodeum reticulate, dorsum with pair of narrow elongate areas extending from proximal margin about one third length of combined dorsum and posterior face; elongate areas flanked anteriorly on each side by triangular area extending

FIGURES 3.9-3.12. *Photomorphus schoenwerthi,* **sp. nov.**, 9. habitus; 10. head, frontal view; 11. mesosternum; and 12. pygidium.

from proximal margins posteriorly about half their length. Reticulations of dorsum and posterior face of propodeum extending laterally. Anterior area of mesopleura nitid, with sparse punctures ventrally and becoming closely punctured dorsally. Elevated area of



FIGURES 3.13-3.18. *Odontophotopsis dalyi*, **sp. nov.**, genitalia, 13. ventral view , 14. dorsal view; *Odontophotopsis odontolaxia*, **sp. nov.**, genitalia, 15. ventral view, 16. dorsal view; and *Photomorphus schoenwerthi*, **sp. nov.**, genitalia, 17. ventral view, 18. dorsal view.

mesopleura with moderately large contiguous punctures. Metapleuron polished. Mesosternum (Fig. 3.11) with pair of high, transverse, oblique, compressed elevations; anterior face of each elevation convex; posterior face of each concave; each elevation bears weak carinulate ridge posteriorly. Each elevation with transverse groove at apex. Mid and hind coxa edentate. Mid femur not swollen. Marginal cell on costa short, ~1.3 × length of stigma. Marginal cell subtruncate apically.

Metasoma (Fig. 3.9). First metasomal segment subsessile with second segment. T1 nitid with close punctures. Disk of T2 nitid with small, sparse punctures becoming closely punctate at anterior, posterior and lateral margins. S2 with felt line, 0.3 × length of tergal felt line. Felt line area of T2 and S2 concolorous with surrounding integument.

Pygidium (Fig. 3.12) elongate and ovate, granulate, margined laterally with carinae; Hypopygidium elongate and ovate; apical margin tridentate medially. Genitalia

(Figs 3.17 and 3.18) with paramere acicular; cuspis elongate, approximately 0.66 × free length of paramere, and cylindrical in lateral view basally, apical 0.75 elongate paddle-shaped, with moderate dorsal basal pit. Penal valve obscured in lateral view by elongate parapenial lobes.

Length. 10 – 12.5 mm.

Female. Unknown.

Material examined. Holotype data, ♂: USA, Arizona, *Yavapai Co.*, 2 mi E Montezuma Well, 19-20.Jun.2007, K.A. Williams (EMUS); **Paratypes:** Arizona: *Gila Co.,* Globe, 1 ♂, 9.Jun.1936, F.H. Parker (UAIC), 1 ♂, 20.Jun.1936, F.H. Parker (UMSP), 1 ♂, 28.Jun.1935, F.H. Parker (UMSP), Payson, 3 mi. N, 1 ♂, 23.Jul.1937, Rehn, Pate & Rehn (UMSP); *Maricopa Co.*, Phoenix, 1 ♂, 17.May.1942 (UMSP), 1 ♂, 29.Jn.1924, J.H. O'Dell (UMSP); *Mojave Co.*, Hualpa Mts., W. S1, 1 ♂, 8.Aug.1962, F. Werner & J. Bequaert (UAIC); *Pima Co*., Baboquivari Campground, 1 ♂, 11 mi E Topawa, 1 ♂, 31.Jun.2011, K.A. & E.E. Williams (EMUS); Saguaro National Monument: 1 ♂, 28.Apr.1961, 1 ♂, 30.Apr.1961, 1 ♂, 2.May.1960, 1 ♂, 5.May.1961, 4 ♂, 7May.1960, 1 ♂, 18.May.1961, 1 ♂, 26.May.1960, 4 ♂, 27.May.1960, 3 ♂, 30.May.1961, 3 ♂, 1.Jun.1960, 1 ♂, 2.Jun.1960, 1 ♂, 12.Jun.1960, G.D. Butler (UAIC); Tucson, 1 ♂, 7.May.1958, G.D. Butler (UAIC), 1 ♂, 20.May.1935, Bryant (UMSP); Vail, 8 mi N, 1 ♂, 26.Jun1962, F. Werner (UAIC); *Yavapai Co*., 2 mi E Montezuma Well, 29 ♂, 19-20.Jun.2007, K.A. Williams (EMUS); *Yuma Co.*, Kofa National Wildlife Reserve, 2 ♂, 1.May.2010, E.E. & K.A.Williams (EMUS); Yuma Proving Grounds, Site 531.8, 1 ♂, 26.May.2001, S.L. Buchmann (EMUS).

Other material examined. USA, California, JTNP, 18–21.Jul.2012, 1 ♂ S18.

Distribution. USA (Arizona and California).

Activity. This species was too rare at JTNP to assess its activity patterns.

Etymology. Named in honor of Franz Xaver von Schönwerth (1810 – 1886), who has now been recognized as an important collector of folklore in the Bavarian region of Germany after unpublished material collected by him, including some 500 folktales, was discovered in Regensburg by Erika Eichenseer in 2009.

***Schusterphotopsis barghesti* Pitts, 2003**

Schusterphotopsis barghesti Pitts, 2003. Zootaxa 333: 3-5. ♂. Holotype data: California, San Bernardino County, 13 mi SE Lucerne Valley, 5000', 2.Aug.1969, D.P. Levin (EMUS).

Diagnosis of male. The genus and species can be distinguished from males of other sphaeropthalmine species by the dilated and deeply emarginated condition of the mandibles (see Pitts 2003: Fig. 1), the posterior position of the mesosternal processes (see Pitts 2003: Figs. 4, 5), the presence of lateral carinae on the hypopygidium (see Pitts 2003: Fig. 3) and the flattened condition of the hypopygidium.

Female. Unknown.

Material Examined. Holotype data: California, San Bernardino County, 13 mi SE Lucerne Valley, 5000', 2.Aug.1969, D.P. Levin (EMUS).

Distribution. USA (California).

Activity. This species was not collected during the course of this study.

Remarks. This species is known from the single specimen from Lucerne Valley, California, but may possibly be found in JTNP at higher elevations. This genus and its taxonomic placement are discussed in Pitts (2003).

***Sphaeropthalma amphion* (Fox, 1899)**

Mutilla amphion Fox, 1899. Amer. Ent. Soc., Trans. 25: 263. ♂. Syntype data: Nevada (ANSP).

Photopsis abstrusa Baker, 1905. Invertebrata Pacifica 1: 113. ♂. Syntype data: California (CUIC). Synonymized by Ferguson (1967).

Photopsis nudata Baker, 1905. Invertebrata Pacifica 1: 114. ♂. Holotype data: Claremont, California (CUIC). Synonymized by Ferguson (1967).

Diagnosis of male. The male of this species has the mandible with a somewhat tapered apex and with the dorsal carina becoming obsolete distally such that the distal portion of mandible is oblique (see Pitts *et al*. 2010a: Fig. 15). Also, the marginal cell length is short being 0.5–0.9 × length of stigma, and this species lacks a sternal felt line. In addition to the mandibular morphology, the genitalia are diagnostic. The cuspis is elongate (0.7–0.8 × free length of paramere) and is dilated towards its apex and has the ventral portion,

especially at the apex and inner margin, clothed with long dense setae that have their apices plumose. Genitalia are illustrated by Pitts *et al.* (2010a: Fig. 52).

Diagnosis of female. The female of this species has the dorsum lacking dense appressed setae obscuring the integumental sculpture, the first segment of the metasoma is sessile with the second segment, the antennal scrobes have dorsal carinae, the mandible has a slightly developed ventral basal tooth and lacks a dorsal tooth at the termination of the dorsal carina, flagellomere 1 is almost 2 × as long as the pedicel, the legs are concolorous with mesosoma, or at most slightly darker or lighter than mesosoma, the propodeum length in lateral view is subequal to 0.5 × maximum height, the metasomal segments have sparse to dense plumose pubescence apically, the apical metasomal segments are concolorous with the basal segments, T2 is coarsely confluently punctate laterally and on basal ~0.66, apical ~0.33 with sparse indiscernible punctures, the pygidium undefined laterally by carinae, and plumose setae are present on the metasomal fringes.

Material examined. *Mutilla amphion* Syntype data: Nevada (ANSP). *Photopsis abstrusa* Syntype data: California (CUIC). *Photopsis nudata* Holotype data: Claremont, California (CUIC). JTNP: 18–21.Jul.2012: 2 ♂ N9; 1 ♂ N5. 26–28.Aug.2012: 1 ♂ N9; 2 ♂ N7; 2 ♂ N5; 1 ♂ N3; 2 ♂ N1; 14 ♂ T; 24 ♂ S1; 13 ♂ S3; 2 ♂ S5; 1 ♂ S7; 2 ♂ S11; 6 ♂ S13; 2 ♂ S18. 22–24.Sep.2012: 1 ♂ N7; 1 ♂ N5; 2 ♂ N1; 2 ♂ T; 9 ♂ S1; 1 ♂ S3; 2 ♂ S7; 3 ♂ S9; 3 ♂ S13; 7 ♂ S18. 26–28.Oct.2012: 1 ♂ N1; 1 ♂ S1.

Distribution. USA (Arizona, California, Nevada, Baja California, Mexico, Nevada, Oregon, and Utah).

Activity. This species is seemingly active later in the season at JTNP.

Remarks. This species is widespread throughout much of the western United States (e.g. Pitts *et al.* 2004; Pitts *et al.* 2010a) and seems more abundant at JTNP (Table 2 & 3) than further north in the Mojave Desert (e.g. Ferguson 1967; Wilson *et al.* 2010; Boehme *et al.* 2012). This species is in the *S. uro* species-group (Pitts & Sadler 2015). Host data and a more detailed treatment of the taxonomy for this species are presented in Pitts *et al.* (2004).

***Sphaeropthalma angulifera* Schuster, 1958**

Sphaeropthalma (*Photopsis*) *angulifera* Schuster, 1958. Ent. Amer. 37: 32. ♂. Holotype data: California, Kern County, Bakersfield (CASC).

Diagnosis of male. The male of this species has mandibles that are weakly excised ventrally with a distinct angulate basal tooth and an apex that is tridentate and oblique, but most importantly the dorsal carina of the mandible is angulate at the midpoint of the mandible coinciding with the ventral tooth (see Pitts *et al.* 2010a: Fig. 54), the posterior margin of the head is quadrate, the mesosternum lacks processes, the second metasomal sternum has a distinct felt line, and the pygidium is granulate. The genitalia also help to diagnose this species; the cuspis is a uniform diameter from the base to the apex (see Pitts *et al*. 2010a: Fig. 53).

Diagnosis of female. The female of this species has the dorsum of the body covered with moderately dense erect pale golden brachyplumose setae that do not obscure the integument; the ventral margin of the mandible has a slight excision followed by a distinct angulate tooth and lacks a dorsal tooth at the termination of the dorsal carina; the head below the eyes widens towards the mandibular insertions; the first metasomal segment is sessile with the second; the pygidium is granulate; and the apical margins of the terga have dense fringes of white plumose setae.

Material examined. Holotype data: California, Kern County, Bakersfield (CASC). JTNP: 18–21.Jul.2012: 3 ♂ N9; 1 ♂ S18. 26–28.Aug.2012: 2 ♂ N9; 1 ♂ T. 22–24.Sep.2012: 2 ♂ N9; 1 ♂ T. 26–28.Oct.2012: 9 ♂ N9; 9 ♂ N5; 1 ♂ S13; 5 ♂ S18.

Distribution. USA (California, and Nevada).

Activity. This species is seemingly active throughout the season but is rare at JTNP.

Remarks. *Sphaeropthalma angulifera* is in the *S. unicolor* species-group (Pitts & Sadler 2015) and is morphologically similar to *S. unicolor* (Cresson, 1865) and *S. mendica*, but can be differentiated from these two species by mandibular morphology (Wilson & Pitts 2009). Although this species is found throughout the Mojave and western Sonoran Deserts, it is extremely rare. Wilson & Pitts (2009) diagnosed the female based on associations made from similarities of the female to that of *S. mendica* and distributional data. This species is typically rare, but seems more abundant at JTNP (Table 3.2 & 3.3) than further north in the Mojave Desert (e.g. Ferguson 1967; Boehme *et al.* 2012) or south into the Sonoran Desert (e.g. Pitts *et al.* 2010a).

***Sphaeropthalma arota* species-complex (Cresson, 1875)**

Mutilla Arota Cresson, 1875. Amer. Ent. Soc., Trans. 5: 120. ♀. Holotype data: California, San Diego (UMSP).

Mutilla helicaon Fox, 1899. Amer. Ent. Soc., Trans. 25: 254. ♂. Holotype data: Nevada (UMSP). Synonymized by Pitts *et al.* (2009).

Photopsis lingulatus Viereck, 1902. Acad. Nat. Sci. Phil., Proc. 54: 737. ♂. Holotype data: California, San Diego County, La Jolla (UMSP). Synonymized by Pitts *et al.* (2009).

Sphaeropthalma (*Photopsis*) *carinata* Schuster, 1958. Ent. Amer. 37: 34. ♂. Holotype data: Baja California, Purissima (NMNH). Synonymized by Pitts *et al.* (2009).

Sphaeropthalma (*Photopsis*) *helicaon coahuilae* Schuster, 1958. Ent. Amer. 37: 34. ♂. Holotype data: lost. Synonymized by Pitts *et al.* (2009).

Sphaeropthalma (*Photopsis*) *helicaon diegueno* Schuster, 1958. Ent. Amer. 37: 35. ♂. Holotype data: Arizona, S. Carlos (CUIC). Synonymized by Pitts *et al.* (2009).

Diagnosis of male. This species has a weak excision and slight angulate tooth on the ventral margin of the mandible (see Pitts *et al.* 2009: Fig. 102), the apex of the mandible is oblique, the clypeus being carinate at base, but sometimes delicately so or gibbous, the lack of mesosternal processes or a sternal felt line, and the ventral margin of the paramere having dense setae that are directed inward toward the cuspis (see Pitts *et al.* 2009: Fig. 100).

Diagnosis of female. The female of this species has the following combination of characters: the mandible has only a weak angulate basal tooth on the ventral margin and lacks a dorsal tooth at the termination of the dorsal carina (see Boehme *et al.* 2012: Fig. 40, Pitts *et al.* 2009: Fig. 40), the mesosoma and second tergum of the metasoma is covered in brachyplumose orange setae surrounded by white setae along the margins (see Pitts *et al.* 2009: Figs 97, 98), the dorsum lacks dense appressed setae obscuring the integumental sculpture, the metasoma is petiolate, and the pygidium is granulate.

Material examined. *Mutilla Arota* Holotype data: California, San Diego, G.R. Crotch, Type no. 1873 (UMSP). *Mutilla helicaon* Holotype data: Nevada, Type no. 4642 (UMSP). *Photopsis lingulatus* Holotype data: California, San Diego County, La Jolla (UMSP). *Sphaeropthalma* (*Photopsis*) *carinata* Holotype data: Baja California, Purissima (NMNH). *Sphaeropthalma* (*Photopsis*) *helicaon diegueno*. Holotype data: Arizona, S. Carlos, 12–13 May 1918, J. Ch. Bradley (CUIC). JTNP: 18–21.Jul.2012: 1 ♂ N7; 1 ♂ N1; 2 ♂ S18. 26–28.Aug.2012: 5 ♂ T; 3 ♂ S1; 3 ♂ S3; 1 ♂ S5; 2 ♂ S13; 4 ♂ S18. 22–24.Sep.2012: 3 ♂ S1; 1 ♂ S5; 1 ♂ S7; 1 ♂ S13; 2 ♂ S18.

Distribution. USA (Arizona, California, Colorado, Nevada, New Mexico, Texas, and Utah) and northern Mexico (Baja California, Chihuahua, Coahuila, and Sonora).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. Wilson *et al.* (2012) performed a phylogenetic analysis of this species. The study concluded that *S. arota* is composed of four genetically distinct species that cannot be distinguished morphologically based on current methods and suggested that the members of this group be identified as the *S. arota* species-complex. Currently it is

placed in the *S. arota* species-group (Pitts & Sadler 2015). From this study, it is likely that only one of the species occurs at JTNP. This complex of species can be locally abundant (Table 3.2 & 3.3; e.g. Pitts *et al.* 2009, 2010a; Wilson *et al.* 2012), but is often rare (Wilson *et al.* 2010).

***Sphaeropthalma becki* Ferguson, 1967**

Sphaeropthalma (*Micromutilla*) *becki* Ferguson, 1967. Brigham Young Univ. Sci. Bull. Biol. Ser. 8: 9. ♂. Holotype data: Nevada, Nye County, Hillside, 0.85 mi NNW Mercury (NMNH).

Diagnosis of male. This species has a deeply excised mandible with the tooth forming an oblique angle (see Pitts *et al*. 2009: Fig. 45), lacks of mesosternal processes, has the marginal cell shorter than the stigma, has the first segment of the metasoma petiolate with the second segment, and has the genitalia with a short cylindrical cuspis (see Pitts *et al*. 2009: Fig. 2).

Female. Unknown.

Material examined. Holotype data: Nevada, Nye County, Hillside, 0.85 mi NNW Mercury, 23 Aug 1964, W.E. Ferguson (NMNH). JTNP: 18–21.Jul.2012: 2 ♂ N7; 7 ♂ N5; 11 ♂ N3; 8 ♂ N1; 34 ♂ T; 12 ♂ S1; 40 ♂ S3; 30 ♂ S5; 19 ♂ S7; 9 ♂ S9; 43 ♂ S11; 41 ♂ S13; 54 ♂ S18. 26–28.Aug.2012: 2 ♂ N3; 3 ♂ N1; 4 ♂ S3; 2 ♂ S5; 4 ♂ S7; 4 ♂ S11; 3 ♂ S13; 2 ♂ S18. 22–24.Sep.2012: 1 ♂ S1; 4 ♂ S3; 3 ♂ S11; 1 ♂ S18.

Distribution. USA (Arizona, California, and Nevada).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. This is the smallest species of nocturnal mutillid found at JTNP. It is placed in the *S. difficilis* species-group (Pitts & Sadler 2015) and abundant throughout its range (Table 2 & 3; e.g. Ferguson 1967; Pitts *et al.* 2009, 2010a; Wilson *et al.* 2010; Boehme *et al.* 2012).

***Sphaeropthalma blakeii* (Fox, 1893)**

Photopsis Blakeii Fox, 1893. Calif. Acad. Sci., Proc. 4: 6. ♂. Lectotype data: Baja California, San Jose del Cabo (ANSP).

Mutilla Gautschii Dalla Torre, 1897. Cat. Hym. 50. New name erroneously proposed for *Photopsis Blakeii* Fox, thought to be preoccupied by Cameron, 1894.

Mutilla ceyx Fox, 1899. Amer. Ent. Soc., Trans. 25: 262. ♂. Lectotype data: Calmili Mines (ANSP). Synonymized by Ferguson (1967).

Diagnosis of male. This species is easily recognized by the posterior margin of the head being quadrate, by the weakly excised mandible that is dilated apically (see Pitts *et al*. 2009: Fig. 37), by the large stigma that is slightly longer than the marginal cell, by the denticles on the internal margin of the hind coxa, by the lack of mesosternal processes, by the quadrate pygidium, and by the lobate dorsoventrally flattened condition of the cuspis,

which has long setae along the internal margin that coalesce apically (see Pitts *et al*. 2009: Fig. 23).

Diagnosis of female. The female of this species can be diagnosed by the following combination of characters: the dorsum of the body is covered with sparse erect brachyplumose setae, but the integument is not obscured, the ventral margin of the mandible lacks an excision and lacks a dorsal tooth at the termination of the dorsal carina, the head below eyes is parallel, the head evenly rounded in lateral view, the first metasomal segment is sessile with the second segment and the pygidium is granulate.

Material examined. Lectotype data: Baja California, San Jose del Cabo (ANSP). JTNP: 18–21.Jul.2012: 3 ♂ N9; 3 ♂ N7; 12 ♂ N5; 6 ♂ N3; 3 ♂ N1; 1 ♂ T; 1 ♂ S7; 1 ♂ S11; 12 ♂ S18. 26–28.Aug.2012: 1 ♂ N7; 2 ♂ N3; 1 ♂ S1; 6 ♂ S3; 1 ♂ S5; 2 ♂ S9; 1 ♂ S11; 2 ♂ S13; 1 ♂ S18. 22–24.Sep.2012: 8 ♂ N9; 6 ♂ N7; 25 ♂ N5; 58 ♂ N3; 1 ♂ N1; 1 ♂ T; 13 ♂ S1; 13 ♂ S3; 4 ♂ S5; 9 ♂ S7; 13 ♂ S9; 15 ♂ S11; 54 ♂ S13; 77 ♂ S18. 26–28.Oct.2012: 4 ♂ N1; 1 ♂ S1; 10 ♂ S5; 8 ♂ S7; 16 ♂ S9; 1 ♂ S11; 2 ♂ S13; 3 ♂ S18.

Distribution. USA (Arizona, California, Nevada and Utah) and northern Mexico (Baja California and Sonora).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. Pitts *et al.* (2009) recently associated the sexes of this species and discussed the taxonomy. It is placed in the *S. blakeii* species-group (Pitts & Sadler 2015) and is abundant throughout its range (Table 3.2 & 3.3; e.g. Ferguson 1967; Pitts *et al.* 2009, 2010a; Wilson *et al.* 2010; Boehme *et al.* 2012).

***Sphaeropthalma difficilis* (Baker, 1905)**

Photopsis difficilis Baker, 1905. Invertebrata Pacifica 1: 114. ♂. Holotype data: California Claremont (CUIC).

Sphaeropthalma (*Micromutilla*) *maricopella purismella* Schuster, 1958. Ent. Amer. 37: 17. ♂. Holotype data: Lost. Synonymized by Ferguson (1967).

Sphaeropthalma (*Micromutilla*) *maricopella maricopella* Schuster, 1958. Ent. Amer. 37: 17. ♂. Holotype data: Lost. Synonymized by Ferguson (1967).

Sphaeropthalma (*Micromutilla*) *maricopella castanea* Schuster, 1958. Ent. Amer. 37: 17. ♂. Holotype data: Lost. Synonymized by Ferguson (1967).

Sphaeropthalma (*Micromutilla*) *californiense californiense* Schuster, 1958. Ent. Amer. 37: 18. ♂. Holotype data: Lost. Synonymized by Ferguson (1967).

Sphaeropthalma (*Micromutilla*) *californiense fuscatella* Schuster, 1958. Ent. Amer. 37: 18. ♂. Holotype data: Lost. Synonymized by Ferguson (1967).

Sphaeropthalma (*Micromutilla*) *quijotoa quijotoa* Schuster, 1958. Ent. Amer. 37: 18. ♂. Holotype data: Lost. Synonymized by Ferguson (1967).

Sphaeropthalma (*Micromutilla*) *quijotoa parrasia* Schuster, 1958. Ent. Amer. 37: 18. ♂. Holotype data: Lost. Synonymized by Ferguson (1967).

Diagnosis of male. This species has a deeply excised vertical mandible with the tooth forming an acute angle (see Pitts *et al*. 2009: Fig. 38), lacks mesosternal processes, and has the marginal cell shorter than the stigma, the first segment of the metasoma petiolate

with the second segment and densely punctate, the second sternum with an anteromedial tumid region, and the genitalia with a long cylindrical cuspis that is setose ventrally with the apex having longer denser setae and parameres with dense setae located medially, but internally directed, along the internal margin (see Pitts *et al*. 2009: Fig. 3).

Diagnosis of female. The female of this species has the dorsum of the body covered with sparse erect brachyplumose setae, but the integument is not obscured, the ventral margin of the mandible with a deep excision subtended by a large rounded tooth and lacks a dorsal tooth at the termination of the dorsal carina, the head below eyes is parallel, the head evenly rounded in lateral view, the first metasoma segment is petiolate with the second segment and the pygidium is striate to granulate.

Material examined. Holotype data: California Claremont (CUIC). JTNP: 18–21.Jul.2012: 17 ♂ N9; 24 ♂ N7; 38 ♂ N5; 15 ♂ N3; 3 ♂ N1; 25 ♂ T; 37 ♂ S1; 21 ♂ S3; 10 ♂ S5; 6 ♂ S7; 5 ♂ S9; 26 ♂ S11; 8 ♂ S13; 65 ♂ S18. 26–28.Aug.2012: 1 ♂ N9; 9 ♂ N7; 2 ♂ N5; 5 ♂ N3; 4 ♂ N1; 3 ♂ T; 13 ♂ S1; 24 ♂ S3; 20 ♂ S5; 56 ♂ S7; 17 ♂ S9; 25 ♂ S11; 15 ♂ S13; 15 ♂ S18. 22–24.Sep.2012: 2 ♂ N9; 4 ♂ N7; 3 ♂ N5; 20 ♂ N3; 10 ♂ N1; 11 ♂ T; 12 ♂ S1; 25 ♂ S3; 27 ♂ S5; 46 ♂ S7; 62 ♂ S9; 12 ♂ S11; 44 ♂ S13; 23 ♂ S18. 26–28.Oct.2012: 3 ♂ S7; 5 ♂ S9; 3 ♂ S18.

Distribution. USA (Arizona, California, Colorado, Idaho, Nevada, New Mexico, Oregon, and Utah) and northern Mexico (Baja California and Sonora).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. Wilson & Pitts (2012) performed a phylogenetic analysis of *S. difficilis* and used this species to identify potential Pleistocene refugia in the North American cold

deserts. Their research on this species provided evidence that in addition to desert-like conditions persisting through the ice age in parts of the Nearctic warm deserts, many areas maintained desert-like characteristics in the regional cold deserts. It is abundant throughout its range (Table 3.2 & 3.3; Ferguson 1967; Pitts *et al.* 2009, 2010a; Wilson *et al.* 2010; Wilson & Pitts 2012; Boehme *et al.* 2012). This species is closely related to *S. django*, which is restricted to the Algodones Sand Dunes (Pitts *et al.* 2009).

Although most of the holotypes of the Schuster species synonymized with *S. difficilis* are listed as "lost", they were likely never labeled as holotypes (Ferguson 1967). This holds for most other Schuster types that are missing as well.

This species is currently placed in the *S. difficilis* species-group (Pitts & Sadler 2015).

***Sphaeropthalma fergusoni* Pitts, 2010, in Pitts *et al.* (2010)**

Sphaeropthalma fergusoni Pitts, 2010, in Pitts *et al.* (2010). Zootaxa, 2553: 21–23. ♂.

Holotype data: California, Riverside County, Corn Springs, 24.Jun.2004, K.A. Williams (EMUS).

Diagnosis of male. This species can be recognized by its quadrate head, the thickened apex of the clypeus (see Pitts *et al.* 2010a: Fig. 41), the mid coxa with a median denticle present on the inner margin and diagnostic genitalia with which it shares features

only with *S. arnalduri* Pitts (see Pitts *et al.* 2010a: Fig. 65), while lacking any mesosternal processes.

Female. Unknown.

Material examined. Holotype data: California, *Riverside Co.*, Corn Springs, 24.Jun.2004, K.A. Williams (EMUS). JTNP: 18–21.Jul.2012: 1 ♂ N9; 1 ♂ S18. 26–28.Aug.2012: 2 ♂ N3; 1 ♂ N1; 52 ♂ T; 69 ♂ S1; 7 ♂ S3; 1 ♂ S5; 5 ♂ S7; 2 ♂ S9; 3 ♂ S11; 5 ♂ S13; 4 ♂ S18.22–24.Sep.2012: 1 ♂ N7; 1 ♂ S1; 2 ♂ S18. 26–28.Oct.2012: 2 ♂ S18.

Distribution. USA (California).

Activity. This species is seemingly active later in the season at JTNP.

Remarks. The distribution of this species was previously known only from two sites (Pitts *et al.* 2010a). It is quite abundant at JTNP (Table 3.2 & 3.3). The mandible looks similar to that of *S. angulifera.* However, their genitalia differ drastically, with the most obvious difference being that *S. angulifera* has the cuspis cylindrical, while *S. fergusoni* has it dorsoventrally flattened. This species is currently placed in the *S. fergusoni* species-group (Pitts & Sadler 2015) along with *S. arnalduri* Pitts, 2010. In order for this species to key out correctly in Pitts *et al.* (2010a), the following modifications need to be made to the species key on page 29:

4. Hind or mid coxae with lobes or denticles.....5

-. Hind and mid coxae unmodified 9

5. Hind or mid coxae with denticles 6

-. Hind coxae with lobes 7

***Sphaeropthalma macswaini* Ferguson, 1967**

Sphaeropthalma (*Micromutilla*) *macswaini* Ferguson, 1967. Brigham Young Univ. Sci. Bul., Biol. Ser. 8, no. 4: 12. ♂. Holotype data: Nevada, Nye County, 2.1 mi NE Mercury (NMNH).

Diagnosis of male. This species has distinctive tridentate mandibles that are deeply excised ventrally and the apex is vertical and greatly dilated, which is similar to species of *Acrophotopsis* and *Dilophotopsis*, but more so than other species at Deep Canyon (see Pitts *et al*. 2010a: Fig. 24). Additionally, the clypeus is distinctly elongate and projects anteriorly and the genitalia have a distinctively shaped curved cuspis that bears a large setal filled pit (see Pitts *et al*. 2010a: Fig. 58). This species sometimes has weak mesosternal processes located anteromedially.

Female. Unknown.

Material examined. Holotype data: Nevada, Nye County, 2.1 mi NE Mercury, 24 August 1964, W.E. Ferguson (NMNH). JTNP: 18–21.Jul.2012: 1 ♂ N1; 27 ♂ T. 26–28.Aug.2012: 2 ♂ N1; 5 ♂ T; 8 ♂ S1. 22–24.Sep.2012: 2 ♂ S1.

Distribution. USA (Arizona, California, Nevada, and Utah)

Activity. This species is seemingly active throughout the season but is somewhat rare at JTNP.

Remarks. The clypeus of this species is diagnostic (Pitts *et al.* 2010a). However, it is elongate and the extreme apex overlies the greatly dilated and deeply excised

mandibles, but does not obscure them. Additional taxonomy for this species is presented by Pitts *et al.* (2010a). This species is in the *S. difficilis* species-group (Pitts & Sadler 2015) and it seems to be more abundant in the southern extent of the Mojave (Table 3.2 & 3.3) and into the Sonoran Desert (e.g. Pitts *et al.* 2010a; Wilson *et al.* 2010). For this study, it was collected only around the transition zone.

***Sphaeropthalma marpesia* (Blake, 1879)**

Mutilla Marpesia Blake, 1879. Amer. Ent. Soc., Trans. 7: 247. ♀. Syntype data: Kansas; Utah (ANSP).

Sphaerophthalma [sic.] *luteola* Blake, 1886. Amer. Ent. Soc., Trans. 13: 235. ♀. Syntype data: Kansas; Utah (ANSP). Synonymized by Krombein (1951).

Sphaeropthalma (*Photopsis*) *imperialiformis* Viereck, 1906. Amer. Ent. Soc., Trans. 32: 189. ♂. Holotype data: Kansas, Morton Co. (SEMC). Synonymized by Pitts (2006).

Sphaeropthalma (*Photopsis*) *imperialiformis imperialiformis* (Viereck) in Schuster, 1958. Ent. Amer. (n. s.) 37: 34. ♂. Synonymized by Pitts (2006).

Sphaeropthalma (*Photopsis*) *imperialiformis maricopae* Schuster, 1958. Ent. Amer. (n. s.) 37: 34. ♂. Holotype data: Arizona, Phoenix (UMSP). Synonymized by Pitts (2006).

Diagnosis of male. This species can be separated from all other nocturnal species by its lack of mesosternal processes and by its coloration; the integument is black throughout except metasomal segments 3–6 are orangish and by the setal coloration of the vertex, pronotum, mesonotum and metasomal segment 2 that varies from silver to orange. The mandible is moderately dilated, distally little or scarcely wider than at tooth, the ventral basal tooth of the mandible is small, and the apex is vertical (see Pitts, 2006: Fig. 6) Also, the head is quadrate posteriorly being long and parallel behind the eyes (see Pitts, 2006: Fig. 2), the clypeus is deeply depressed below the dorsal mandibular margin, the sternal felt line is present, and by characteristic genitalic morphology (see Pitts 2006: Figs 14–16).

Diagnosis of female. This species is easily recognized by its unique color pattern (see Pitts, 2006: Fig. 25). Other useful characters include the petiolate metasomal segment 1, the small ventral angulation located basally on the mandible, the granulate pygidium, and the presence of plumose setae especially on the fringes of the metasomal terga.

Material examined. *Mutilla Marpesia* Syntype data: Kansas, Type no. 4542 (ANSP). *Sphaeropthalma* (*Photopsis*) *imperialiformis* Holotype data: Kansas, Morton Co., 3200', June 1902, F.H. Snow (SEMC). *Sphaeropthalma* (*Photopsis*) *imperialiformis maricopae* Holotype data: Arizona, Phoenix, 25 September 1935, R.H. Crandall (UMSP).

Distribution. USA (Arizona, California, Colorado, Idaho, Kansas, Nevada, New Mexico, Oklahoma, Oregon, Texas, Utah, and Washington) and northern Mexico (Sonora).

Activity. This species was not collected during the course of this study.

Remarks. No specimens of this species were seen from JTNP (Table 3.2 & 3.3), but given that it occurs all around the park and throughout the Southwest, it likely occurs at JTNP as well. Pitts (2006) associated the females of this species and discussed the taxonomy of this species, as well as other members of the *S. imperialis* species-group (Pitts & Sadler 2015).

***Sphaeropthalma megagnathos* Schuster, 1958**

Sphaeropthalma (*Photopsis*) *megagnathos megagnathos* Schuster, 1958. Ent. Amer. (n. s.) 37: 36. ♂. Holotype data: Arizona, Ehrenberg (UMSP).

Sphaeropthalma (*Photopsis*) *megagnathos aurifera* Schuster, 1958. Ent. Amer. (n. s.) 37: 36. ♂. Holotype data: Arizona, Tinajas Atlas Mountains (UMSP). Synonymized by Pitts (2006).

Diagnosis of male. This species can be separated from all other nocturnal species by mandibular morphology: the mandibles are very broadly dilated, especially ventral portion apically, distally much wider than width at ventral angulation, the ventral basal tooth of the mandible is small, and the apex is vertical (see Pitts 2006: Fig. 7). Also, the head is long and parallel posteriorly, the clypeus is deeply depressed below the dorsal mandibular margin, the mesosternum lacks tubercles, the wings are yellowish-hyaline, and the sternal felt line is absent. The genitalic morphology also is diagnostic (see Pitts

2006: Figs 17–19). In some specimens the coloration of the integument and setae are bright orange, while in others the setal coloration varies from orange to white and the integument is stramineous to castaneous.

Diagnosis of female. This species has weak to non–existent ventral angulation located basally on the mandible while the mandible lacks an elongate tooth at the termination of the dorsal carina, distinctly petiolate metasomal segment 1, the granulate pygidium, presence of plumose setae especially on the fringes of the metasomal terga, the sparse long orange setae that does not obscure the integumental sculpturing and the anterior raised areas just lateral of the midline on the second tergum that has tuberculate sculpturing.

Material examined. *Sphaeropthalma* (*Photopsis*) *megagnathos megagnathos* Holotype data: Arizona, Ehrenberg, 27 April 1939, F.H. Parker (UMSP). *Sphaeropthalma* (*Photopsis*) *megagnathos aurifera* Holotype data: Arizona, Tinajas Atlas Mountains, 1905, W.J. McGee (UMSP). JTNP: 18–21.Jul.2012: 10 ♂ S18. 26–28.Aug.2012: 2 ♂ S1; 1 ♂ S18.

Distribution. USA (Arizona, California, and Nevada).

Activity. This species is seemingly active earlier in the season, but is rare at JTNP.

Remarks. The female of this species was described in Boehme *et al.* (2012), where it was found to be more abundant than elsewhere (e.g. Wilson *et al.* 2010). Pitts (2006) treated the taxonomy of this species in more detail along with other members of the *S. imperialis* species-group (Pitts & Sadler 2015).

***Sphaeropthalma mendica* (Blake, 1871)**

Agama mendica Blake, 1871. Amer. Ent. Soc., Trans. 3: 259. ♂. Syntype data: Nevada (ANSP).

Mutilla aspasia Blake, 1879. Amer. Ent. Soc., Trans. 7: 250. ♀. Holotype data: Nevada (ANSP). Synonymized by Ferguson (1967).

Photopsis nebulosus Blake, 1886. Amer. Ent. Soc., Trans. 13: 275. ♂. Holotype data: Nevada (ANSP). Synonymized by Ferguson (1967).

Diagnosis of male. This species has mandibles that are weakly excised ventrally with a indistinct basal tooth and an apex that is tridentate and oblique (see Pitts *et al*. 2010a: Fig. 55), the posterior margin of the head is quadrate, the mesosternum lacks processes, the second metasomal sternum has a distinct felt line, and the pygidium is granulate. The genitalia of this species are quite similar to those of *S. angulifera*. Genitalia are illustrated by Pitts *et al.* (2010a: Fig. 60).

Diagnosis of female. This species has the dorsum of the body covered with dense erect red to pale orange brachyplumose setae that obscure the integument; the ventral margin of the mandible has a slight excision, but lacks a ventral tooth and a dorsal tooth at termination of dorsal carina; the head below the eyes widens towards the mandibular insertions; the first metasoma segment is sessile with the second segment; and the pygidium is longitudinally striate and granulate between the striae; the eyes are larger than the distance from the posterior margin of the eye to the vertex of the head (the eye is

from 1.2 to 1.4 times as big as the length from the margin of the eye to the vertex of the head); and the apical margins of the terga have dense fringes of white plumose setae.

Material examined. *Agama mendica* Syntype data: Nevada, type no. 4551 (ANSP). *Mutilla aspasia* Holotype data: Nevada, type no. 4574 (ANSP). *Photopsis nebulosus* Holotype data: Nevada, type no. 4549 (ANSP). JTNP: 18–21.Jul.2012: 1 ♂ N5; 3 ♂ N3; 2 ♂ N1; 1 ♂ T; 3 ♂ S1; 1 ♂ S3; 2 ♂ S13; 110 ♂ S18. 26–28.Aug.2012: 1 ♂ N7; 2 ♂ T; 11 ♂ S1; 1 ♂ S13; 14 ♂ S18. 22–24.Sep.2012: 1 ♂ T; 1 ♂ S1; 1 ♂ S3; 5 ♂ S9; 4 ♂ S13; 30 ♂ S18. 26–28.Oct.2012: 1 ♂ S1.

Distribution. USA (Arizona, California, Colorado, Idaho, Nevada, and Utah).

Activity. This species is seemingly active throughout the season at JTNP.

Remarks. There is a wide array of integumental coloration in this species (Wilson & Pitts 2009). Specimens range from nearly black integument to a more reddish-brown color characteristic of most nocturnal mutillids. Female integumental coloration has a range similar to the males. At JTNP only the reddish-brown color form was collected. This species is a member of the *S. unicolor* species-group (Pitts & Sadler 2015) and is typically abundant throughout its range (Table 3.2 & 3.3).

***Sphaeropthalma militaris* Schuster, 1958**

Sphaeropthalma (*Photopsis*) *militaris* Schuster, 1958. Ent. Amer. 37: 27. ♂. Holotype data: California, Riverside County, Hopkins Well, 29.May.1952, G.A. Marsh (CASC).

Diagnosis of male. This species has a deep excision on the ventral margin of the mandible, the mandible being tridentate and vertical apically, the dense brush of orangish setae projecting forward off of the anterior margin of the clypeus (see Pitts *et al.* 2009: Fig. 93), the lack of mesosternal processes, and the genitalia, which has a dorsoventrally flattened paramere that are thickly setose apically and a cylindrical cuspis that is approximately ¾ the free length of the paramere (see Pitts *et al.* 2009: Fig. 25).

Diagnosis of female. This species has the dorsum of the body covered with sparse erect brachyplumose setae, but the integument is not obscured, the ventral margin of the mandible with a deep excision subtended by a large rounded tooth, the head below eyes convergent, the frons evenly rounded to the vertex in lateral view, the first metasoma segment is petiolate with the second segment and the pygidium is granulate.

Material examined. Holotype data: California, Riverside County, Hopkins Well, 29.May.1952, G.A. Marsh (CASC). USA: California: San Bernardino County: Joshua Tree National Park, Dale Mine, 1 ♂, 25.May.2012, F. & T. Cambon (EMUS).

Distribution. USA (Arizona and California).

Activity. This species is rare at JTNP.

Remarks. This species is a member of the *S. orestes* species-group and is more abundant in the Sonoran Desert (e.g. Pitts *et al.* 2009, 2010a; Wilson *et al.* 2010).

***Sphaeropthalma nana* (Ashmead, 1896)**

Photopsis nanus Ashmead, 1896: 181, ♂. Lectotype: Arizona, Tucson (NMNH); Pitts *et al.* 2004: 224, ♂ (as type species of *Micromutilla* Ashmead).

Mutilla acontius Fox, 1899: 266, ♂. Lectotype: New Mexico, Las Cruces (ANSP).

Mutilla Ashmeadii Fox, 1899: 289. Replacement name for *Photopsis nanus* Ashmead, 1896, nec *Mutilla nana* Smith 1879.

Photopsis nana Ashmead: Lelej & Brothers 2008: 35, ♂ (as type species of *Micromutilla* Ashmead).

Diagnosis of male. This species can be recognized by its small size, the moderately emarginate mandibles (see Pitts 2007: Fig. 27), the small marginal cell, which is shorter than the stigma measured along the costal margin, the lack of mesosternal processes, the genitalia with an extremely short cuspis that barely surpasses the penial valve in lateral view, and the lack of plumose setae even along the margins of the metasomal terga. Genitalia are illustrated in Boehme *et al.* (2012: Fig. 9).

Female. Unknown.

Material examined. Lectotype data: *Ph. nanus*: Arizona, Tucson, type no. 3279 (NMNH); Lectotype data: *M. acontius*: New Mexico, Las Cruces, type no. 3279 (ANSP). JTNP: 18–21.Jul.2012: 1 ♂ N7.

Distribution. USA (Arizona, California, Nevada and New Mexico) and northern Mexico (Baja California and Sonora).

Activity. This species is seemingly rare at JTNP.

Remarks. Boehme *et al.* (2012) designated the Lectotype, and reinstated the name for stability and to lessen potential confusion based on article 59.3 of ICZN (1999). See Boehme *et al.* (2012) for the complicated taxonomic history of this species. This species is a member of the *S. nana* species-group (Pitts & Sadler 2015) and is typically rare (Table 2 & 3; e.g. Ferguson 1967; Pitts *et al.* 2009; Boehme *et al.* 2012).

***Sphaeropthalma orestes* (Fox, 1899)**

Mutilla orestes Fox, 1899. Amer. Ent. Soc., Trans. 25: 256. ♂. Holotype data: no locality data (ANSP).

Mutilla Pattersonae Melander, 1903. Amer. Ent. Soc., Trans. 29: 309. ♂. Holotype data: California, Fort Washington, 3 October 1895, R. Patterson (NMNH). Synonymized by Schuster (1958).

Photopsis indigens Baker, 1905. Invertebrata Pacifica 1: 112. ♂. Holotype data: King's Canon, Ormsby Co., Nevada (CUIC). Synonymized by Schuster (1958).

Photopsis uniformis Baker, 1905. Invertebrata Pacifica 1: 113. ♂. Syntype data: California, Claremont (CUIC). Synonymized by Schuster (1958).

Photopsis pedatus Baker, 1905. Invertebrata Pacifica 1: 115. ♂. Syntype data: California, Claremont (CUIC). Synonymized by Schuster (1958).

Photopsis ingenuus Baker, 1905. Invertebrata Pacifica 1: 116. ♂. Holotype data: California, Claremont (CUIC). Synonymized by Schuster (1958).

Photopsis salmani Mickel, 1938. Pan–Pacific Ent. 14: 178. ♂. Holotype data: California, Eagle Lake, 30 July 1936, C.E. Mickel (UMSP). Synonymized by Ferguson (1962).

Sphaeropthalma (Photopsis) salmani fresnoensis Schuster, 1958. Ent. Amer. (n. s.) 37: 30. ♂. Holotype data: lost. Synonymized by Ferguson (1962).

Sphaeropthalma (Photopsis) salmani oregano Schuster, 1958. Ent. Amer. (n. s.) 37: 31. ♂. Holotype data: lost. Synonymized by Ferguson (1962).

Diagnosis of male. This species has mandibles that are strongly excised ventrally, have a vertical face, have a distinct basal tooth and an apex that is tridentate and oblique (see Boehme *et al.* 2012: Fig. 19), the posterior margin of the head is rounded, the mesosternum lacks processes, the second metasomal sternum lacks a distinct felt line, the pygidium is glabrous and the cuspis of the genitalia spatulate and lack plumose setae. Genitalia are illustrated in Boehme *et al.* (2012: Fig. 10).

Diagnosis of female. This species has the dorsum of the body covered with sparse erect brachyplumose setae, but the integument is not obscured, the ventral margin of the mandible bears a large ventral basal tooth but lacks a dorsal tooth at the termination of the dorsal carina, the head below eyes is parallel, the head evenly rounded in lateral view, the first metasoma segment is petiolate with the second segment and the pygidium is granulate.

Material examined. *Mutilla orestes* Holotype data: no locality data (ANSP). *Mutilla Pattersonae* Holotype data: California, Fort Washington, 3 October 1895, R. Patterson (NMNH). *Photopsis uniformis* Syntype data: California, Claremont (CUIC).

Photopsis pedatus Syntype data: California, Claremont (CUIC). *Photopsis ingenuus* Holotype data: California, Claremont (CUIC). *Photopsis salmani* Holotype data: California, Eagle Lake, 30 July 1936, C.E. Mickel (UMSP).

Distribution. USA (Arizona, California, Colorado, Idaho, Nevada, New Mexico, Oregon, Utah and Washington) and northern Mexico (Baja California and Sonora).

Activity. No specimens of this species were collected during the course of this study.

Remarks. This species is a member of the *S. orestes* species-group (Pitts & Sadler 2015). The absence of *S. orestes* at the JTNP is odd because the species is known to be abundant throughout its range, which extends west of the Rocky Mountains from mainland Mexico to southern Canada. It was the second most abundant species at AMNWR (Boehme *et al.* 2012). It likely occurs in JTNP.

***Sphaeropthalma pallidipes* Schuster, 1958**

Sphaeropthalma (*Photopsis*) *pallidipes pallidipes* Schuster, 1958: 27. ♂. Holotype data: Lost.

Sphaeropthalma (*Photopsis*) *pallidipes gila* Schuster, 1958: 28. ♂. Holotype data: Lost. Synonymized by Mickel (1974).

Diagnosis of male. This species has deeply excised mandibles having the apex oblique and the dorsal carina terminating well before the apex, the lack of a sternal felt line, lack

of mesosternal processes, the pronotum and second metasomal segment that is sometimes darkened, and genitalic morphology. The cuspis is almost as long as the paramere with long curved spinulae on the inner margin from the base to the apex and short spinulae elsewhere. The parameres have long curved spinulae on the inner margin that are thicker medially than proximally or distally and have short spinulae on the outer margin.

Female. Unknown.

Material examined. JTNP: 26–28.Aug.2012: 4 ♂ S5; 10 ♂ S7; 7 ♂ S9; 1 ♂ S13.22–24.Sep.2012: 3 ♂ S5; 2 ♂ S7.

Distribution. USA (Arizona, California, and New Mexico) and northern Mexico (Sonora).

Activity. This species is seemingly active later in the season at JTNP.

Remarks. This species is a member of the *S. orestes* species-group (Pitts & Sadler 2015). Mickel (1974) synonymized the subspecies with which we agree. Paratypes of both subspecies exist at UMSP from Tucson, AZ (subspecies *pallidipes*) and from San Carlos, AZ and NM (subspecies *gila*). The holotypes were never labeled as such by Schuster. This species was collected only south of the transition zone in the Sonoran Desert during this study.

***Sphaeropthalma parkeri* Schuster, 1958**

Sphaeropthalma (*Photopsis*) *parkeri* Schuster, 1958: 28. ♂. Holotype data: Arizona, Ehrenberg (UMSP).

Diagnosis of male. This species can be recognized by having mandibles that are vertical and are strongly excised ventrally with a distinct basal tooth and an apex that is tridentate and oblique (see Boehme *et al.* 2012: Fig. 20), the posterior margin of the head is rounded, the mesosternum lacks processes, the second metasomal sternum with a distinct tuft-like felt line, S2 with a anteromedial carinate tumid region, the pygidium is glabrous and the cuspis of the genitalia spatulate and lack plumose setae. Genitalia are illustrated in Boehme *et al.* (2012: Fig. 11).

Female. Unknown.

Material examined. Holotype data: Arizona, Ehrenberg, 27.Apr.1939, F.H. Parker (UMSP). USA: California: San Bernardino County: Joshua Tree National Park, Dale Mine, 2 ♂, 25.May.2012, F. & T. Cambon (EMUS).

Distribution. USA (Arizona, California, and Nevada).

Activity. This species is seemingly rare at JTNP.

Remarks. This species is a member of the *S. orestes* species-group (Pitts & Sadler 2015) and has characteristic genitalia with the paramere spatulate with ventral setae. It is rare throughout its range (Table 3.2 & 3.3).

***Sphaeropthalma sublobata* Schuster, 1958**

Sphaeropthalma (*Micromutilla*) *sublobata* Schuster, 1958. Ent. Amer. (n. s.) 37: 16. ♂.

Holotype data: Mt. Home, Idaho, 7.Jul.1951, J. Nottingham (SEMC).

Diagnosis of male. This species can be recognized by the weakly excised mandibles that are oblique apically (see Pitts *et al.* 2010a: Fig. 28), a marginal cell that is approximately 0.75 × the length of the stigma, the mesosternum lacks processes, the first metasomal segment is sessile with the second, plumose setal fringes are present on the metasoma, the hind coxa has large lobes, the pygidium glabrous, and the cuspis of the genitalia is thickened, densely setose, and long being approximately 0.75 × the free length of the paramere (see Pitts *et al.* 2010a: Fig. 62).

Female. Unknown.

Material examined. Holotype data: Mt. Home, Idaho, 7.Jul.1951, J. Nottingham (SEMC). USA: California: San Bernardino County: Joshua Tree National Park, Dale Mine, 2 ♂, 25.May.2012, F. & T. Cambon (EMUS). JTNP: 18–21.Jul.2012: 1 ♂ T.

Distribution. USA (Arizona, California, Idaho, Nevada and Utah).

Activity. This species is seemingly rare throughout its range.

Remarks. Schuster designated a holotype from Mt. Home, Idaho. He also designated a holotype from Ehrenberg, Arizona located in UMSP. This second holotype is not conspecific with the first holotype and does not match the characters Schuster (1958) listed for this species in his key. This species is a member of the *S. brachyptera* species-group (Pitts & Sadler 2015) and is seemingly rare throughout its range (Table 3.2 & 3.3).

***Sphaeropthalma triangularis* (Blake, 1871)**

Agama triangularis Blake, 1871. Amer. Ent. Soc., Trans. 3: 262. ♂. Holotype data: Nevada (ANSP).

Diagnosis of male. This species is easily recognized by the lobe-like projections on the hind coxae. Other useful characters include the triangular shaped posterior margin of the head, the weakly excised mandible (see Pitts *et al*. 2009: Fig. 40), the lack of mesosternal processes, and the unique triangulate posterior projection of the apex of the hind tibia. Genitalia are illustrated by Pitts *et al.* (2009: Fig. 26).

Diagnosis of female. This species has the dorsum of the body covered with sparse erect brachyplumose setae, but the integument is not obscured; the ventral margin of the mandible has a slight excision, but lacks a long erect tooth at the termination of the dorsal carina; the head below eyes is parallel; the head evenly rounded in lateral view; the first metasomal segment is sessile with the second segment; and the pygidium is longitudinally striate.

Material examined. Holotype data: Nevada (ANSP). JTNP: 18–21.Jul.2012: 1 ♂ N5. 26–28.Oct.2012: 1 ♂ S9.

Distribution. USA (Arizona, California, Nevada, New Mexico, Utah and Texas) and northern Mexico (Baja California and Sonora).

Activity. This species is seemingly rare at JTNP.

Remarks. This species is placed in its own species-group (Pitts & Sadler 2015), and seems to be closely related to members of the *S. unicolor species-group* (e.g. Pitts et al. 2010b). It also seems to be more abundant at the northern extent of its range (Table 3.2 & 3.3; Pitts *et al.* 2009, 2010a; Wilson *et al.* 2010; Boehme *et al.* 2012).

***Sphaeropthalma uro* (Blake, 1879)**

Agama uro Blake, 1879. Amer. Ent. Soc., Trans. 7: 253. ♂. Syntype data: Texas (ANSP).

Photopsis melanderi Baker, 1905. Invertebrata Pacifica 1: 112. ♂. Holotype data: Texas, Coryell Co. (CUIC). Synonymized by Krombein (1979).

Sphaeropthalma (*Photopsioides*) *uro stenognatha* Schuster, 1958. Ent. Amer. (n. s.) 37: 38. ♂. Holotype data: Arizona, St. Carlos (UMSP). Synonymized by Krombein (1979).

Diagnosis of male. This species can be recognized by the mandible, which is slightly to very broadly dilated apically, has a sharp dorsal carina that is blade-like to apex of mandible such that the mandible vertical throughout, but has a weak ventral emargination and tooth (see Boehme *et al.* 2012: Fig. 21). Also, the clypeus is strongly depressed, the anterior margin hidden below dorsal mandibular rims, the head is quadrate posteriorly, the marginal cell is 0.75–1.0X the length of the stigma, S2 lacks a felt line and the cuspis of the genitalia are broadly spatulate and bear plumose setae (see Pitts *et al.* 2004: Figs 19–21).

Diagnosis of female. This species has the dorsum lacking dense appressed setae that obscures the integumental sculpture, the first segment of the metasoma is sessile with the second segment, the antennal scrobes have dorsal carinae, the mandible has a slightly developed ventral basal tooth and lacks a dorsal tooth at the termination of the dorsal carina, flagellomere 1 is almost 2 × as long as the pedicel, the legs are concolorous with mesosoma or at most slightly infuscated or lighter than mesosoma, the propodeum length in lateral view is subequal to 0.5 × maximum height, the metasomal segments have sparse plumose pubescence apically and the apical metasomal segments are concolorous with basal metasomal segments, T2 is coarsely punctate throughout with the interstitial distance less than a puncture width and the pygidium is undefined laterally by carinae.

Material examined. *Agama uro* Syntype data: Texas (ANSP). *Photopsis melanderi* Holotype data: Texas, Coryell Co., Birkman (CUIC). *Sphaeropthalma (Photopsioides) uro stenognatha* Holotype data: Arizona, St. Carlos, 27 August 1935, F.H. Parker (UMSP).

Distribution. USA (Arizona, California, Kansas, Nevada New Mexico and Utah) and northern Mexico (Baja California and Sonora).

Activity. No specimens of this species were collected during the course of this study.

Remarks. No specimens of this species were seen from JTNP (Table 3.2 & 3.3), but given that it occurs all around the park and throughout the Southwest, it likely occurs at JTNP as well. Host data and a more detailed treatment of the taxonomy for this

member of the *S. uro* species-group (Pitts & Sadler 2015) are presented in Pitts *et al.* (2004).

***Sphaeropthalma yumaella* Schuster, 1958**

Sphaeropthalma (*Micromutilla*) *yumaella* Schuster, 1958. Ent. Amer. 37: 19. ♂.

Holotype data: Arizona, Yuma County, Wellton (CUIC).

Diagnosis of male. This species is recognized by the strongly excised mandible (see Pitts *et al*. 2010a: Fig. 31), the lack of mesosternal processes, the marginal cell being shorter than the stigma, the first segment of the metasoma sessile with the second segment, and the genitalia with a long thick cylindrical cuspis that tapers apically and has a large basal pit on the internal margin (see Pitts *et al*. 2009: Fig. 6).

Female. Unknown.

Material examined. Holotype data: Arizona, Yuma County, Wellton (CUIC). JTNP: 18–21.Jul.2012: 1 ♂ N7; 2 ♂ N5; 2 ♂ N3; 6 ♂ T; 21 ♂ S1; 9 ♂ S3; 8 ♂ S5; 5 ♂ S7; 14 ♂ S9; 8 ♂ S11; 2 ♂ S13; 14 ♂ S18. 26–28.Aug.2012: 1 ♂ N9; 1 ♂ N7; 3 ♂ N5; 9 ♂ N3; 4 ♂ N1; 5 ♂ T; 10 ♂ S1; 25 ♂ S3; 36 ♂ S5; 12 ♂ S7; 30 ♂ S9; 17 ♂ S11; 53 ♂ S13; 41 ♂ S18. 22–24.Sep.2012: 1 ♂ N9; 16 ♂ N5; 44 ♂ N3; 22 ♂ N1; 5 ♂ T; 14 ♂ S1; 43 ♂ S3; 26 ♂ S5; 47 ♂ S7; 34 ♂ S9; 25 ♂ S11; 76 ♂ S13; 96 ♂ S18. 26–28.Oct.2012: 4 ♂ S1; 4 ♂ S3; 4 ♂ S5; 13 ♂ S9; 2 ♂ S11; 1 ♂ S13; 9 ♂ S18.

Distribution. USA (Arizona, California, and Nevada) and northern Mexico (Baja California).

Activity. This species is active throughout the season at JTNP.

Remarks. This species is a member of the *S. brachyptera* species-group, which is in desperate need of revision, and is widespread (Pitts *et al.* 2009). Based on mandibular and genitalic morphology, along with wing venation similarities, this species is closely related to *S. brachyptera* Schuster, 1958, *S. noctivaga* (Melander, 1903), *S. sublobata* Schuster, 1958, and *Odontophotopsis piute* Mickel, 1983 (in Mickel & Clausen, 1983). Additional taxonomic description for this species can be found in Pitts *et al.* (2009). This species is seemingly more abundant in the Mojave Desert (Table 3.2 & 3.3) than elsewhere in its range (e.g. Wilson *et al.* 2010).

Key to the male nocturnal mutillids of Joshua Tree National Park

(modified from Boehme *et al.,* 2012)

1. Mesosternum with large, glabrous, longitudinal swellings located on either side of the midline.....*Odontophotopsis mamata* Schuster
-. Mesosternum with spine-like processes, ridges or lacking processes.....2
2. Hind coxae with lobes or denticles.....3
-. Hind coxae unmodified 5
3. Hind coxae with denticles; apex of mandible dilated.... *Sphaeropthalma blakeii* (Fox)
-. Hind coxae with lobes; apex of mandible parallel 4

4. Hind tibia with lateral expansion; posterior margin of head somewhat triangular..... ..... *Sphaeropthalma triangularis* (Blake)

-. Hind tibia without lateral expansion; posterior margin of head rounded..... .....*Sphaeropthalma sublobata* Schuster

5. Mid coxae with denticles; mandible attenuated towards apex; apex of clypeus visible and thickened.....*Sphaeropthalma fergusoni* Pitts

-. Mid coxae without denticles; mandible rarely attenuated towards apex; apex of clypeus not thickened 6

6. Mandible with ventral lamella; lingulate tubercle situated medially at the posterior margin of the clypeus in between the antennal insertions..... ..... *Odontophotopsis unicornis* Schuster

-. Mandible without ventral lamella; without lingulate tubercle situated medially at the posterior margin of the clypeus in between the antennal insertions.....7

7. Clypeus elongate, but not overlapping mandibles; mandible greatly dilated apically and ventrally excised AND MC less than length of stigma measured along wing margin; cuspis with enlarged setal filled pit; integument stramineous .... *Sphaeropthalma macswaini* Ferguson

-. Clypeus not elongate; mandible and MC variable; cuspis lacking enlarged setal filled pit; integument variable.....8

8. Hypopygidium flattened; lateral margins of hypopygidium with longitudinal carinae anteriorly.....9

-. Hypopygidium convex; lateral margins of hypopygidium without longitudinal carinae.....11

9. Mesosternum armed with pair of small, lamellate tooth-like processes, originating near midline immediately anterior to mesocoxae, appearing to slightly cup anterior margin of mesocoxae, mostly impunctate..... *Schusterphotopsis barghesti* Pitts

-. Mesosternum either unarmed or armed with tubercles situated well anterior to mesocoxae 10

10. Mesosternum without tubercles; cuspis not elbowed..... *Acrophotopsis dirce* (Fox)

-. Mesosternum with conical tubercles; cuspis elbowed..... ..... *Dilophotopsis paron* (Cameron)

11. Mesosternum armed with spines or ridges 12

-. Mesosternum unarmed, lacking spines or ridges 32

12. Mandible quadridentate, with three apical teeth and a fourth tooth along internal margin that overhangs clypeus; cuspis of genitalia knobbed apically; mesosternal teeth enlarged, somewhat laterally flattened triangulate spines ....*Acanthophotopsis falciformis* Schuster

-. Mandible apex bidentate, tridentate, or quadridentate, but without a fourth tooth along internal margin that overhangs clypeus; cuspis of genitalia tapering apically; mesosternal teeth variable but not laterally flattened triangulate spines.....13

13. Mesosternal tubercles with transverse apical groove.....14

-. Mesosternal tubercles without a transverse apical groove 15

14. Setae of mesoscutum golden; cuspis elongate, approximately 0.66 × free length of paramere; fore wing with apical maculation .... *Photomorphus schoenwerthi* Sadler & Pitts, **sp. nov.**

-. Setae of mesoscutum pale white; cuspis shorter, approximately 0.5 × free length of paramere fore wing usually without maculation .... *Photomorphus clandestina* (Viereck)

15. Mandible greatly dilated with large dorsal tooth separated from other teeth by a deep, wide sinus (see Pitts 2007: Fig. 27) 16

-. Mandible variable, but without a deep, wide sinus 17

16. Clypeus with dense, short, even-length brush of stiff, subclavate setae; clypeus without horseshoe-shaped posteromedially process; mandible quadridentate distally .. .. *Odontophotopsis setifera* Schuster

-. Clypeus virtually glabrous; clypeus with horseshoe-shaped tubercle posteromedially that overhangs the clypeus as a slight hood-like or nasutiform process; mandible tridentate distally ..... *Odontophotopsis biramosa* Schuster

17. Mesosternum armed with two teeth on each side, situated in almost a square with posterior teeth slightly further apart than anterior teeth AND MC as long as or longer than the stigma measured on the margin .....*Odontophotopsis quadridentata* Schuster

-. Mesosternum variously armed with a single pair of teeth with one tooth on each side, although in some cases the teeth may be bifid, or in one case compound; MC length variable 18

18. Ventral margin of mandible with deep excision subtended by a large rounded tooth....
.....19

-. Ventral margin of mandible with weak excision subtended by angulation or small rounded tooth (if questionable, pygidium granulate) 27

19. Pygidium granulate; mesosternal processes bifid..... *Odontophotopsis bellona* Mickel

-. Pygidium glabrous (if granulate, then body size small, coloration light stramineous, and genitalia with elongate cylindrical cuspis bearing long sparse setae ventrally: *O. quadrispinosa*); mesosternum with either a single tooth on each side of the midline, or with two teeth on each side of the midline separated by a distance greater than their height and forming a square.....20

20. Marginal cell approximately 0.5 × length of stigma; mesosternum usually with two teeth on each side of the midline separated by a distance greater than their height and forming a square, sometimes posterior set of teeth indistinct; genitalia with elongate cylindrical cuspis bearing long sparse setae ventrally.....
.....*Odontophotopsis quadrispinosa* Schuster

-. Marginal cell approximately equal to or longer than the length of stigma; mesosternum with only a single tooth on each side of the midline; cuspis of genitalia variable, but not bearing long sparse setae just ventrally.....21

21. Clypeus posteromedially tuberculate; apex of the mandible slightly oblique; sternal felt line absent or vestigial..... *Odontophotopsis armata* Mickel

-. Clypeus lacking posteromedial tubercle; apex of the mandible and sternal felt line variable 22

22. Second sternum lacking a felt line..... *Odontophotopsis serca* Viereck

-. Second sternum with a felt line 23

23. Posterior margin of head quadrate; clypeus depressed below dorsal margin of mandible, appearing concave ..... *Odontophotopsis melicausa* (Blake)

-. Posterior margin of head rounded; clypeus level with dorsal margin of mandible or slightly below it 24

24. Clypeus elongate and flattened, plate-like … *Odontophotopsis obscura* Schuster

-. Clypeus not elongate or flattened 25

25. Apex of mandible slightly less than vertical; mesosternal processes situated anteromedially 26

-. Apex of mandible obviously not vertical, rotated half way between vertical and horizontal (45º to 60º); mesosternal processes situated approximately more lateral and slightly more posterior than for previous species .....
..... *Odontophotopsis microdonta* Ferguson

26. Metasoma darkened at least under felt lines; mesosternal processes strong .....
..... *Odontophotopsis clypeata* Schuster

-. Metasoma not darkened; mesosternal processes weak.....
..... *Odontophotopsis delodonta* Viereck

27. Mandible with third (dorsal) tooth expanded dorsally .....
..... *Odontophotopsis odontoloxia* Sadler & Pitts, **sp. nov.**

-. Mandible with third (dorsal) tooth not expanded 28

28. Ventral margin of mandible with sudden vertical deep excision; mesosternal processes bifid ..... *Odontophotopsis bellona* Mickel

-. Excision of ventral margin of mandible shallow, with small subtending tooth; mesosternal processes various (if bifid, ventral mandibular tooth shallow) 29

29. Felt lines of S2 small vestigial tufts or lacking; metasternum trilobite..... ..... *Odontophotopsis inconspicua* (Blake)

-. Felt lines of S2 well-developed; metasternum bilobate.....30

30. Mesosternal processes high and conspicuous 31

-. Mesosternal processes low and inconspicuous..... *Odontophotopsis aufidia* Mickel

31. Mesosternal process rounded distally, separated by a deep V-shaped sinus; pygidium margined by a distinct carina; apex of mandible not dilated..... ..... *Odontophotopsis parva* Schuster

-. Mesosternal process bifid distally, separated by a deep U-shaped sinus; pygidium not margined; apex of mandible dilated ..... *Odontophotopsis acmaea* Viereck

32. Clypeus surpasses closed mandibles AND mandible with a weak or nonexistent ventral excision..... *Odontophotopsis sonora* Schuster

-. Clypeus does not surpasses closed mandible OR mandible with distinct ventral excision.....33

33. Second sternum completely lacking felt line.....34

-. Second sternum with felt line, appearing either as an elongate line or as a tuft of dense setae 40

34. Mandible with a weak ventral excision and small ventral tooth 38

-. Mandible with a strong ventral excision and large ventral tooth 35

35. Clypeus hidden under a dense brush of golden stiff setae .....
.....*Sphaeropthalma militaris* Schuster

-. Clypeus not hidden, with sparse setae only.....36

36. Mandible appearing attenuated towards apex because tridentate apex oblique .....
.....*Sphaeropthalma pallidipes* Schuster

-. Mandible apex vertical and slightly dilated apically.....*Sphaeropthalma orestes* (Fox)

37. Cuspis of genitalia cylindrical, setae simple throughout.....38

-. Cuspis of genitalia dorsoventrally flattened, spatulate, with ventral setae plumose towards apex.....39

38. Clypeus lacking medial raised area or longitudinal carina posteriorly; mandible broadly dilated, especially ventral portion apically, distally much wider than width at ventral angulation, apex vertical (see Pitts 2006: Fig. 7); clypeus deeply depressed below mandibular rims; parameres lacking large tuft of inward directed setae along ventral margin at base of paramere (see Pitts 2006: Fig. 19); head quadrate posteriorly.....*Sphaeropthalma megagnathos* Schuster

-. Clypeus with medial raised area or longitudinal carina present posteriorly; mandible not dilated apically, apex oblique; clypeus not depressed below mandibular rims; parameres with inward directed setae along ventral margin at base of paramere; head rounded posteriorly.....*Sphaeropthalma arota* (Cresson)

39. Mandible with dorsal carina sharp, blade-like to apex of mandible, mandible vertical throughout; length of clypeal apical truncation greater than 0.6 × width ....*Sphaeropthalma uro* (Blake)

-. Mandible with dorsal carina becoming obsolete distally, distal portion of mandible oblique; length of clypeal apical truncation less than 0.5 × width .... *Sphaeropthalma amphion* (Fox)

40. Felt line just a tuft of setae 41

-. Felt line more well developed than above, appearing as an elongate line of setae 42

41. Mandible weakly excised ventrally (see Pitts 2006: Fig. 6); second metasomal segment and mesosoma black or blackish and second segment with pubescence variable from orange to silver (see Pitts 2006: Fig. 28); S2 lacking a mediobasal longitudinal timidity ..... *Sphaeropthalma marpesia* (Blake)

-. Mandible strongly excised ventrally; integument stramineous to castaneous, metasoma not darkened even under felt lines; S2 with a mediobasal longitudinal timidity .....*Sphaeropthalma parkeri* Schuster

42. Mandible with the dorsal ridge angulately produced about half-way between base and apex, the dorsal carina suddenly becoming obsolete towards apex..... .....*Sphaeropthalma angulifera* Schuster

-. Mandible without the dorsal ridge angulately produced about half-way between base and apex, the dorsal carina gradually becoming obsolete 43

43. Pygidium granulate.....44

-. Pygidium glabrous.....46

44. Cuspis elongate, approximately 0.75 × free length of paramere, with sparse elongate setae ventrally; mandible vertical; body size small ..... *Odontophotopsis quadrispinosa* Schuster

-. Cuspis short to elongate, if elongate, mandible oblique and body size large 45

45. Mandible apex oblique; cuspis longer than 0.5 × free length of paramere ..... *Sphaeropthalma mendica* (Blake)

-. Mandible apex vertical; cuspis shorter than 0.5 × free length of paramere ..... *Odontophotopsis dalyi* Sadler and Pitts, **sp. nov.**

46. Cuspis of genitalia ~0.5 × free length of paramere; marginal cell ~1.25 × length of stigma measured along margin; metasoma with dense white plumose fringes, integument usually castaneous around felt lines ..... *Odontophotopsis microdonta* Ferguson

-. Cuspis of genitalia length various; marginal cell length equal to or shorter than that of stigma; metasoma with weak white plumose fringes or lacking them altogether..... 47

47. Angle formed by ventral mandibular excision obtuse (greater than 90º); cuspis of genitalia ~0.5 × free length of paramere ..... *Sphaeropthalma becki* Ferguson

-. Angle formed by ventral mandibular excision acute (less than 90º); cuspis of genitalia much longer or much shorter than ~0.5 × free length of paramere 48

48. T2–6 lacking fringes of plumose setae; cuspis of genitalia in lateral view slightly surpassing the apex of the penis valve in length (cuspis less than 0.25 × the free length of the paramere)..... *Sphaeropthalma nana* (Ashmead)

-. At least T2 fringed with plumose setae medially; cuspis of genitalia in lateral view greatly surpassing the apex of the penis valve in length (cuspis ~0.75 × the free length of the paramere).....49

49. First segment of metasoma sessile with second segment; cuspis with setae of similar length throughout.....*Sphaeropthalma yumaella* Schuster

-. First segment of metasoma petiolate with second segment; apex of cuspis with a ventral tuft of setae that is longer than at the base of the cuspis ....*Sphaeropthalma difficilis* (Blake)

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CHAPTER 4

FAUNAL STUDY OF THE NOCTURNAL ACULEATE WASPS (HYMENOPTERA) OF THE SONORAN AND MOJAVE DESERTS OF JOSHUA TREE NATIONAL PARK[3]

Abstract

Nocturnal aculeate wasps (Hymenoptera: Chyphotidae, Brachycistidinae (Tiphiidae), and Mutillidae) are abundant in North America's deserts, yet their patterns of diversity are not well studied. Here we report on the diversity of these groups in Joshua Tree National Park (JTNP). Based on collection data from a transect of 14 sampling sites transitioning from the Mojave to the Sonoran deserts, our study shows that there are at least 11 species of *Chyphotes* (Chyphotidae), based on the collection of 1,513 specimens, there are at least 22 species of brachycistidine Tiphiidae in five genera, based on the collection of 13,960 specimens, and at least 35 species of nocturnal mutillids in six genera, based on 8,477 specimens. Brachycistidine Tiphiidae populations peak earlier in the season compared to the other two groups. Also we found an increase in Chyphotidae, Brachycistidinae, and Mutillidae diversity and abundance with decreasing latitude. Several species appear to be spatially restricted to one desert region; others exhibit temporal isolation, only being collected during specific months. Our study suggests that

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JTNP houses a diverse community of nocturnal aculeate wasps with the Sonoran Desert being more diverse than the Mojave Desert.

Key words: Sonoran Desert, Mojave Desert, Transition Zone, USA, Biodiversity, Faunal survey

National Parks and other protected areas can play an important role in the maintenance of biodiversity (Bruner *et al.* 2001). In North America, much of the conservation efforts in National Parks have focused on vertebrates (e.g., Clevenger and Waltho, 2000; Mortiz *et al.* 2008) or on rare plants (e.g., Miller and White 1986; Frank and McNaughton 1992). Despite the conservation focus of National Parks in the United States, little has been published about the diverse insect communities housed in these protected areas.

Joshua Tree National Park (JTNP) is unique in that it contains portions of two distinct desert ecoregions. This park gained U.S. National Park status in 1994 and is large covering 792,623 acres in southeastern California (NPS). The northern regions of JTNP are part of the Mojave Desert and the southern regions are in the Colorado Desert subunit of the Sonoran Desert. These two deserts that exist within JTNP, and the transition zone connecting them, provide a unique opportunity to study patterns of insect biodiversity in a potentially diverse ecotone.

Nocturnal aculeate wasps (Hymenoptera: Chyphotidae, Brachycistidinae (Tiphiidae), and Mutillidae) are ubiquitous in North America's deserts, and, although it is

expected that they would play an important part in the ecology of these areas, their patterns of diversity, however, are not well studied. *Chyphotes* Blake (Hymenoptera: Chyphotidae) is a genus of wasp that includes many species endemic to the deserts of North America, though some species can be found as far south as Mexico. *Chyphotes* females, as well as the related genera in Typhoctinae, presumably parasitize the larval or pupal stages of Coleoptera, based on phylogenetic relationships, but Brothers and Finnamore (1993) suggested Solifugae based on a single non-peer reviewed record. This is the only sparse natural history information that exists for this group. While the genus has been revised twice previously by Buzicky (1941) and Mickel (1967), the taxonomy remains unsettled, making species identification challenging.

In the southwestern deserts of the USA, nocturnal wasps in the family Tiphiidae (Hymenoptera: Tiphiidae: Brachycistidinae) likely play an important ecological role as parasitoids based on their high abundance. However, little has been published on this group besides taxonomy. Many Brachycistidinae are endemic to specific arid regions of North America (Kimsey and Wasbauer, 2006), though the subfamily and can be found as far south as Costa Rica. Little is known about the natural history of this group, but it is thought that Brachycistidinae females parasitize the larval or pupal stages of Coleoptera, based on a single recent record (Borowiec and Kimsey, 2015).

Mutillidae (Hymenoptera), also known as velvet ants, is a family of wasp that also has species, both diurnal and nocturnal, endemic to the deserts of North America. However, the nocturnal velvet ant fauna of JTNP is poorly known. Velvet ant females parasitize the larval or pupal stages of holometabolous insects, such as Diptera,

Coleoptera and Hymenoptera, with most known hosts being aculeate Hymenoptera (Brothers *et al.* 2000). As with *Chyphotes,* only sparse natural history information exists for most species of velvet ants.

For all three of these groups, the females presumably spend most of their time underground searching for hosts, and, therefore, are encountered less frequently than males. Males of these groups, however, are easily collected as they are attracted to light traps.

The objectives of this study are to determine species diversity of nocturnal aculeate wasps at JTNP, to determine faunal differences between the different deserts of the park, and to determine relative species abundances in the distinct desert regions. Specimens were collected in a transect spanning both deserts and the transition zone. Understanding patterns of diversity in diverse, desert-adapted insects can inform future conservation efforts and will lead to a better understanding of biodiversity in the National Park.

Materials and Methods

Joshua Tree National Park includes the Mojave Desert, Sonoran Desert, and transition zone between the two. These areas can be identified based on their characteristic vegetation. JTNP is named after the Joshua tree (*Yucca brevifolia*), which is endemic to the Mojave Desert and is restricted to the northern portion of the park. This area also houses piñon pine (*Pinus monophylla*), California juniper (*Juniperus californica*), desert scrub oak (*Quercus turbinella*), Tucker's oak (*Quercus john-tuckeri*) and Muller oak

(*Quercus cornelius-mulleri*) (Ricketts *et al.* 1999). The Colorado Desert (subunit of the Sonoran Desert), which can be found in the southern parts of the park below 3,000 feet (910 m), has flora that includes Creosote bush (*Larrea tridentata*), scrub Ocotillo (*Fouquieria splendens*), desert Saltbush (*Atriplex* spp.), *Yucca* and Cholla cactus (*Cylindropuntia bigelovii*) (Ricketts *et al.* 1999).

Within JTNP, Pinto Basin Road served as the perfect transect between the Mojave and Sonoran deserts. Beginning at the park boundary at the North Entrance and continuing along Pinto Basin Road to the Cottonwood Visitor Center, light traps where deployed approximately every three miles (~5 km) (Table 4.1). Trapping along Pinto Basin Road provided a 27 mile (43 km) transect with a 2,386 foot (727 m) change in elevation. This allowed five light traps to be placed in the Mojave Desert; the sites of these traps are designated N9, N7, N5, N3 and N1, where N stands for north of the transition zone and the number represents the distance from the transition zone in miles. This also allowed from one trap in the transition zone (T) and eight traps south of the transition zone in the Sonoran Desert (S1, S3, S5, S7, S9, S11, S13 and S18). Once again, where S stands for south of the transition zone and the number represents the distance from the transition zone in miles.

Specimens were collected from each site using light traps. The light traps consisted of a fluorescent battery-powered camping lantern and small bowls filled with slightly soapy water. Typically, only males were collected by the light traps. Lights were turned on at dusk and off at dawn. Sites were sampled four times, once each month from July-October of 2012 (18-21 July, 26-28 August, 22-24 September, 26-28 October).

Table 4.1. Transect site information.

Site Name	Site Location	Distance From Road Edge (ft)	Elevation (ft)	Dominant Vegetation Type
N9	N34.00482 W116.04924	218	4,160	Joshua Tree
N7	N34.02017 W116.01778	290	3,646	Yucca & Joshua Trees
N5	N33.99412 W116.02134	296	3,914	Yucca & Joshua Trees
N3	N33.97477 W115.99798	196	3,444	Yucca & Creosote
N1	N33.95148 W115.98084	248	2,953	Creosote & Cheesebush
T	N33.94111 W115.96973	193	2,761	Creosote, Mesquite, & Smoke tree
S1	N33.93315 W115.95633	183	2,540	Smoke tree
S3	N33.92409 W115.92458	104	2,069	100% Jumping Cholla
S5	N33.92419 W115.92508	183	1,834	Small Creosote
S7	N33.91169 W115.86460	232	1,774	Small Creosote & Cheesebush
S9	N33.90141 W115.83225	211	1,784	Small Creosote
S11	N33.87896 W115.81215	253	1,993	Creosote & Mormon tea
S13	N33.85631 W115.79056	181	2,231	Creosote
S18	N33.80103 W115.78088	203	2,793	Creosote

During each sampling event, traps were deployed each evening for a total of two to three nights. All collected specimens were stored in 95% ethanol initially, and pinned, labeled, and identified at the Entomological Museum of Utah State University (EMUS). GPS locations were determined for each collection site (Table 4.1).

The species of *Chyphotes* were identified using Buzicky (1941) and Mickel (1967), as well as through the study of type material. The brachycistidine genera of Tiphiidae were identified using Kimsey & Wasbauer (2006) and the reference collection at EMUS identified by Wasbauer. The species of *Acanthetropis* Wasbauer*, Brachycistis* Fox, *Colocistis* Krombein, and *Stilbopogon* Mickel and Krombein were identified using Wasbauer (1966) and Kimsey & Wasbauer (1998, 2013, 2015). The mutillid genera were identified based on previous research at EMUS and the reference collection housed there.

The Sørensen's similarity index (Sørensen, 1948), which is based on presences/absences, was used to determine the similarity between two sites, and the Bray-Curtis dissimilarity index (Bray and Curtis, 1957), which is additionally based on abundances, was used to determine dissimilarity between two sites.

Results and Discussion

Chyphotes *(Chyphotidae)*

Our trapping efforts resulted in the collection of 1,513 specimens representing 11 species (Table 4.2). *Chyphotes aenigmus* Mickel (n=460), *C. melaniceps* (Blake) (n=320) and *C. atriceps* Mickel (n=301) are the most abundant of all the species found at the park. The rarest species, those with less than 10 individuals found throughout the course of the

Table 4.2. Number of individuals of each *Chyphotes* species collected at each site from north to south. Sites beginning with "N" were Mojave Desert sites, those beginning with "S" were Sonoran Desert sites, and "T" indicates a site in the transition zone.

	Collecting Site														
Species	**N9**	**N7**	**N5**	**N3**	**N1**	**T**	**S1**	**S3**	**S5**	**S7**	**S9**	**S11**	**S13**	**S18**	**Total # per spp.**
Chyphotes aenigmus	3	1	1	7	19	25	36	93	47	28	31	27	67	75	460
Chyphotes atriceps	13	43	17	42	15	2	17	5	4	16	15	24	19	69	301
Chyphotes boharti	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Chyphotes calexicensis	-	-	-	-	-	-	-	-	7	14	14	6	3	2	46
Chyphotes californicus	2	2	1	-	37	48	31	2	1	-	-	3	2	10	139
Chyphotes incredulous	-	-	-	-	-	-	-	-	18	31	22	13	3	-	87
Chyphotes melaniceps	-	-	1	1	21	11	59	62	5	7	11	16	41	85	320
Chyphotes attenuates	4	-	5	10	2	-	-	-	1	-	-	-	7	23	52
Chyphotes minisculus	-	-	-	-	7	16	-	-	2	1	1	2	5	1	35
Chyphotes pallidus	-	-	-	-	-	-	-	3	21	33	5	4	-	1	67
Chyphotes **sp. nov.**	-	-	-	-	-	-	-	-	-	1	1	2	-	1	5
Total # per site	22	46	25	60	101	102	143	165	107	131	100	97	147	267	**= 1,513**

study, include only *C. boharti* Mickel (one specimen) and *C.* **sp. nov.** Sadler and Pitts (five specimens), which will be described in a different publication (Sadler *et al.* 2017).

Tiphiidae (Brachycistidinae)

Our trapping efforts resulted in the collection of 13,960 specimens representing 22 species (Table 4.3). The most abundant species collected at JTNP were *Colocistis castanea* (Cresson) (n=2,842), *C. brevis* (Fox) (n=2,241), and *Acanthetropis noctivaga* (n=1,237). The rarest species was *Brachycistis elegantula* Cockerell and Casad (2 specimens) (Table 4.3).

Mutillidae

Our trapping efforts resulted in 35 species in six genera totaling 8,477 specimens (Table 4.4). *Odontophotopsis microdonta* Ferguson (n=1,803), *O. clypeata* Schuster (n=1,036), and *Sphaeopthalma yumaella* Schuster (n=825) are the most abundant of all the species found at the park. The rarest species, those with less than 10 individuals found throughout the course of the study, include *O. dalyi* Sadler and Pitts (4 specimens), *O. obscura* (Cockerell) (3), *O. odontoloxia* Sadler and Pitts (1), *O. parva* Schuster (2), *O. setifera* Schuster (8), *Photomorphus schoenwerthi* Sadler and Pitts (1), *Sphaeropthalma nana* (Ashmead) (1), and *S. triangularis* (Blake) (2) (Table 4.4). *Odontophotopsis setifera* Schuster, and *S. nana* also were considered rare according to surveys of the Ash Meadows National Wild/life Refuge (Boehme *et al.* 2012).

Table 4.3. Number of individuals of each Brachycistidinae species collected at each site from north to south. Sites beginning with "N" were Mojave Desert sites, those beginning with "S" were Sonoran Desert sites, and "T" indicates a site in the transition zone.

	Collecting Site														
Species	**N9**	**N7**	**N5**	**N3**	**N1**	**T**	**S1**	**S3**	**S5**	**S7**	**S9**	**S11**	**S13**	**S18**	**Total # per spp.**
Acanthetropis noctivaga	1	3	4	26	4	7	31	44	90	119	160	110	314	324	1,237
Brachycistis agama	-	-	-	-	-	-	-	-	4	31	5	17	14	-	71
B. curvata	19	21	254	23	1	1	-	17	34	33	29	18	7	4	461
B. elegantula	-	-	-	-	-	-	-	-	-	-	1	-	1	-	2
B. imitans	1	1	4	-	-	-	-	-	-	1	1	1	11	4	24
B. inaequalis	9	13	1	1	1	-	-	-	45	296	66	3	2	-	437
B. linsleyi	26	30	50	35	4	5	9	19	52	101	144	255	235	23	988
B. petiolate	-	-	-	-	-	-	-	-	17	30	36	4	-	-	87
B. timberlakei	1	40	114	74	-	1	1	20	85	194	206	189	137	40	1,102
B. triangularis	7	-	4	3	18	56	61	33	182	120	111	84	77	86	842
B. vigilax	1	4	27	73	-	1	1	6	69	111	156	18	10	9	486
Brachycistina acuta	44	47	21	39	19	11	7	44	125	262	71	135	135	24	984
Colocistis brevis	1	8	4	7	64	89	245	314	418	537	219	180	45	110	2,241
C. castanea	45	63	30	61	106	175	264	54	73	67	52	138	137	1577	2,842
C. crassa	62	16	21	13	3	1	3	2	-	1	9	85	72	34	322
C. eremi	-	1	-	1	14	2	31	132	89	99	48	271	85	113	886
C. themarum	5	8	7	9	45	103	84	18	8	5	5	9	4	2	312
Stilbopogon inermis	-	-	-	-	29	43	29	4	17	9	46	11	2	2	192
S. marcida	-	-	-	-	5	9	9	1	68	52	75	28	21	7	275
S. megalops	-	1	-	-	13	49	20	-	4	2	8	1	1	-	99
S. paupercula	-	-	-	-	1	-	5	-	6	1	4	-	-	-	17
S. perpunctata	-	-	-	-	1	4	1	1	8	24	9	4	-	1	53
Total # per site	222	256	541	365	328	557	801	709	1394	2095	1461	1561	1310	2360	**= 13,960**

Table 4.4. Number of individuals of each Mutillidae species collected at each site from north to south. Sites beginning with "N" were Mojave Desert sites, those beginning with "S" were Sonoran Desert sites, and "T" indicates a site in the transition zone.

	Collecting Site														
Species	**N9**	**N7**	**N5**	**N3**	**N1**	**T**	**S1**	**S3**	**S5**	**S7**	**S9**	**S11**	**S13**	**S18**	**Total # per spp.**
Acanthophotopsis falciformis	-	-	-	-	-	2	3	-	5	2	14	3	3	2	34
Acrophotopsis dirce	1	20	3	5	12	9	7	1	1	-	13	-	1	23	96
Dilophotopsis paron	49	11	41	4	7	5	1	2	-	1	-	6	5	134	266
Odontophotopsis armata	-	11	2	3	20	84	130	6	1	2	2	-	1	3	265
O. bellona	4	5	8	8	2	14	41	77	40	20	45	9	15	49	337
O. biramosa	-	-	-	-	-	-	-	2	4	5	3	6	10	1	31
O. clypeata	1	4	-	5	3	3	49	128	144	203	71	108	107	210	1,036
O. dalyi	-	2	-	-	-	-	-	-	-	2	-	-	-	-	4
O. delodonta	-	2	-	1	-	1	6	7	8	52	48	18	17	1	161
O. inconspicua	-	1	-	5	5	17	104	18	3	10	30	11	13	59	276
O. mamata	-	-	-	-	1	29	75	19	2	6	3	4	2	12	153
O. melicausa	10	15	-	9	-	2	4	-	-	1	-	9	13	23	86
O. microdonta	79	53	76	125	22	19	13	195	23	11	43	724	286	134	1,803
O. obscura	-	-	-	-	-	-	-	-	-	-	3	-	-	-	3
O. odontoloxia	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
O. parva	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2
O. quadrispinosa	-	-	-	3	-	2	7	26	11	20	26	24	4	5	128
O. serca	3	6	1	8	51	256	375	19	5	2	10	17	6	17	776
O. setifera	-	-	-	-	-	-	-	-	-	-	-	-	-	8	8
O. sonora	-	-	-	-	-	-	1	1	1	5	4	-	-	-	12
Photomorphus schoenwerthi	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Sphaeropthalma amphion	3	2	3	1	5	16	34	14	2	3	3	2	9	9	106
S. angulifera	14	-	9	-	-	1	-	-	-	-	-	-	1	6	31
S. arota	-	1	-	-	1	5	6	3	2	1	-	-	3	8	30

Table 4.4. (continued)

Species	N9	N7	N5	N3	N1	T	S1	S3	S5	S7	S9	S11	S13	S18	Total # per spp.
S. becki	-	2	7	13	11	34	13	48	32	23	9	50	44	57	343
S. blakeii	11	10	37	66	8	2	15	19	15	18	31	18	58	93	401
S. difficilis	20	37	43	40	17	39	62	70	57	111	89	63	67	106	821
S. fergusoni	1	1	-	2	1	52	70	7	1	5	2	3	5	9	159
S. macswaini	-	-	-	-	3	32	10	-	-	-	-	-	-	-	45
S. megagnathos	-	-	-	-	-	-	1	-	-	-	-	-	-	11	12
S. mendica	-	1	1	3	2	4	16	2	-	-	5	-	7	154	195
S. nana	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
S. pallidipes	-	-	-	-	-	-	-	-	7	12	7	-	1	-	27
S. triangularis	-	-	1	-	-	-	-	-	-	1	-	-	-	-	2
S. yumaella	2	2	21	55	26	16	49	81	74	64	91	52	132	160	825
Total # per site	198	187	253	356	197	644	1092	745	439	580	554	1127	810	1295	**= 8,477**

Biogeographical and Ecological Trends

There was a trend showing an increase in the abundance and diversity of all three groups with decreasing latitude (i.e., more specimens representing more species were collected at the south end of the park than the north end) with an average 631 specimens per site caught in the Mojave Desert, 1,303 in the transition zone and 2,436 in the Sonoran Desert. Furthermore, the similarity of the sites decreased and the dissimilarity increased as sites are compared from north (Mojave Desert) to south (Sonoran Desert) (Tables 4.5 and 4.6), although some adjacent sites, such as S5, S7, and S11, were quite similar. Furthermore, the average similarity of Mojave Desert sites was 0.818, similarly, the average similarity of the Sonoran Desert sites was 0.856. The average similarity comparing Mojave to Sonoran sites was 0.741. This suggests that the nocturnal wasp faunas are somewhat distinct for the two different desert regions. For nocturnal aculeate wasps, the Sonoran Desert is more diverse than the Mojave Desert, which is the case for other flora and fauna (Phillips *et al.* 2015). Given the number of specimens collected and the parasitic nature of all three of these groups, aculeate nocturnal wasps must be ecologically significant in these deserts reducing the overall numbers of both potential pollinators, predatory hymenopterans, and phytophagous insects.

Interestingly, there were several species that appeared to be restricted to the Sonoran Desert portions of the park. For example, *Chyphotes boharti*, *C. calexicensis* Bradley*, C. pallidus* Buzicky, and *C. incredulus* Mickel, and *C.* **sp. nov.** (Table 4.2), *Brachycistis agama* (Dalla Torre), *B. elegantula*, and *B. petiolata* Fox (Table 4.3), and

Table 4.5. Sørensen's similarity coefficient based on the combined presence/absence data for all three nocturnal groups. A value of 1 indicates the two localities share all of the same species, and a value of 0 indicates they do not share any of the same species. Indices at, or above, 0.90 are bolded.

	N9	**N7**	**N5**	**N3**	**N1**	**T**	**S1**	**S3**	**S5**	**S7**	**S9**	**S11**	**S13**	**S18**
N9														
N7	0.83													
N5	0.87	0.80												
N3	0.84	**0.90**	0.85											
N1	0.72	0.81	0.76	0.80										
T	0.75	0.86	0.76	0.85	0.87									
S1	0.68	0.82	0.69	0.81	0.86	**0.92**								
S3	0.71	0.83	0.75	0.84	0.84	0.88	0.89							
S5	0.63	0.71	0.64	0.73	0.80	0.80	0.81	0.84						
S7	0.63	0.73	0.63	0.74	0.77	0.81	0.82	0.83	**0.91**					
S9	0.59	0.70	0.63	0.74	0.76	0.78	0.79	0.82	**0.90**	**0.91**				
S11	0.69	0.75	0.65	0.77	0.77	0.83	0.80	0.83	0.88	**0.93**	0.88			
S13	0.73	0.81	0.74	0.82	0.82	0.90	0.83	0.84	0.88	0.87	0.86	0.88		
S18	0.72	0.77	0.73	0.81	0.81	0.89	0.86	0.89	0.83	0.84	0.81	0.86	0.89	

Table 4.6. Bray-Curtis dissimilarity coefficient based on the combined abundance data for all three nocturnal groups. Values close to 1 indicate the communities at these locations are completely different, and values close to 0 indicate they are more similar.

	N9	**N7**	**N5**	**N3**	**N1**	**T**	**S1**	**S3**	**S5**	**S7**	**S9**	**S11**	**S13**	**S18**
N9														
N7	0.35													
N5	0.49	0.50												
N3	0.49	0.34	0.41											
N1	0.67	0.59	0.73	0.64										
T	0.83	0.75	0.83	0.75	0.42									
S1	0.87	0.81	0.85	0.76	0.57	0.32								
S3	0.73	0.69	0.73	0.58	0.66	0.66	0.51							
S5	0.80	0.72	0.71	0.61	0.71	0.71	0.59	0.37						
S7	0.86	0.79	0.76	0.70	0.79	0.78	0.67	0.50	0.26					
S9	0.79	0.71	0.67	0.59	0.71	0.71	0.60	0.47	0.31	0.30				
S11	0.77	0.75	0.73	0.65	0.74	0.73	0.66	0.46	0.46	0.46	0.43			
S13	0.73	0.71	0.67	0.57	0.72	0.71	0.66	0.45	0.47	0.51	0.43	0.28		
S18	0.84	0.81	0.82	0.73	0.80	0.76	0.65	0.57	0.65	0.66	0.64	0.62	0.49	

Acanthophotopsis falciformis Schuster*, Odontophotopsis biramosa* Schuster*, O. obscura, O. odontoloxia, O. parva, O. setifera, O. sonora* (Schuster)*, Photomorphus schoenwerthi, Sphaeropthalma megagnathos* Schuster*,* and *S. pallidipes* Schuster (Table 4.4) were only collected from Sonoran Desert sites. Several other species were much more common in the Sonoran Desert, even though limited individuals were also collected north of the transition zone. For example, all five of the *Stilbopogon* species were primarily collected in the Sonoran Desert, with only a few individuals collected more than 1 mile (1.6 km) north of the transition zone. *Chyphotes aenigmus* was collected from every site, but only 31 individuals were collected from the Mojave region, while 404 individuals were collected from the Sonoran. Some species of mutillids, such as *O. clypeata*, *O. delodonta* Viereck, and *O. inconspicua* (Blake) showed a similar trend. Other species seemed to be most abundant in the transition between Mojave and Sonoran regions. For example, *Stilbopogon megalops* Kimsey and Wasbauer, and *Colocistis themarum* (Bradley), while collected from both deserts, was more abundant in the transition zone site and sites adjacent to it. *Chyphotes californicus* Baker, while collected from both deserts, was found in higher abundance in the transition zone or in the sites adjacent to it. Surprisingly, none of the species collected were restricted to the Mojave Desert portions of the park, though one, *Brachycistis curvata* Malloch, was more abundant in the Mojave sites than in the Sonoran sites.

The diversity of wasps was not even across the collecting dates. Unsurprisingly, the number of individuals collected decreased as the season progressed. For example, 8,287 brachycistidines were collected in July, 2563 in August, 2,727 in September and

383 in October. While overall there was a decrease in abundance as the summer progressed, this pattern was not consistent across all species. Some species, like *Colocistis brevis* and *Co. castanea*, were more commonly collected in the July. Other species, like *Brachycistis agama* and *B. curvata*, were more often collected in September or October, and *Ch. pallidus* and *Acanthophotopsis falciformis* were more commonly collected in the later summer months (Aug and Sep) than in July. Additionally, brachycistidine tiphiids peaked earlier in the season compared to that of the other two groups. This suggests that in addition to the observation that some species are spatially isolated, some species also appear to be temporally isolated.

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CHAPTER 5

COMPARATIVE HISTORICAL BIOGEOGRAPHY OF THE AMERICAN SOUTHWEST WITH EMPHASIS ON THE BAJA PENINSULAR SEAWAY BASED ON THREE GROUPS OF NOCTURNAL WASPS (HYMENOPTERA: CHYPHOTIDAE, MUTILLIDAE AND TIPHIIDAE)[4]

Abstract

The influence of historical climatic and geological changes on patterns of species diversification was investigated in three widely distributed groups of North American nocturnal wasps (Hymenoptera) from the families Chyphotidae, Mutillidae (Sphaeropthalminae) and Tiphiidae (Brachycistidinae) with particular focus on diversification patterns during the Neogene uplift and Pleistocene glacial cycles. We collected molecular data from ultra-conserved elements (UCE) to produce the first phylogenies of *Chyphotes* (Chyphotidae) and *Brachycistis* (Tiphiidae) based on molecular data. Maximum likelihood inference of the UCE data returned two well-resolved trees with bootstrap values of 100 for all but two nodes. For sphaeropthalmine mutillids, we collected molecular data from two nuclear intergenic regions (internal transcribed spacer regions 1 and 2; >2600 bp in total) to add to those published by Pitts *et al.* 2010 to produce a more complete phylogeny of the desert endemic genus *Odontophotopsis* (Mutillidae). Bayesian inference of the combined data of

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Odontophotopsis returned a well-resolved tree with posterior probabilities of over 95% for most nodes. Dates of species divergences for each wasp group were estimated using BEAST and were calibrated with a Dominican amber fossil. For *Odontophotopsis*, the derived dates ranged from the Pleistocene to the Middle Miocene, suggesting that both recent Pleistocene glaciation cycles and older orogenic events, albeit to a somewhat greater extent, were both causes of major diversification in western North America. Although the derived dates also ranged from the Pleistocene to the Middle Miocene for *Chyphotes*, this genus differs from *Odontophotopsis* in that recent Pleistocene glaciation cycles are seemingly the major cause of diversification in western North America. Dates for *Brachycistis* range from the Middle Miocene to the Late Pliocene, and older Neogene orogenic events seem to be the cause of diversification in western North America. Examination of other phylogeographical studies using North American desert taxa indicated that diversification patterns are often explained by either mountain building or Pleistocene climate change, depending on the taxa in question. Species-level relationships support inundation of southern California by the Boues Sea Embayment and a hypothesized Baja Inner Peninsular Seaway.

Key Words: Comparative Phylogeography, Historical Biogeography, diversification, phylogenomics, Refugia

1. Introduction

The North American deserts have long interested evolutionary biologists and biogeographers, because of the region's diverse topography and equally diverse biota. The enormous diversification of the North American desert biota can be linked to geological events, especially those that lead to the formation of the deserts. The existence and timing of specific events, such as the Baja Inner Peninsular Seaway, have been debated by geologists and historical biogeographers (Wilson and Pitts, 2010). The majority of investigations into the historical biogeography of the North American deserts have been accomplished using vertebrate taxa (e.g., Riddle, 1995; Orange *et al.*, 1999; Riddle *et al.*, 2000a; Riddle *et al.*, 2000b; Zink *et al.*, 2001; Jaeger *et al.*, 2005; Devitt, 2006; Douglas *et al.*, 2006; Riddle and Hafner, 2006). Work conducted with these taxa often resulted in conflicting and convoluted views of the causes of diversification, and whether older or more recent geological events are more important to diversification is often debated. Without a more widespread examination of multiple taxa over similar regions a consensus of the actual reasons and multiplicity of causes for diversification cannot be agreed upon.

Some phylogeographic analyses have been performed using invertebrate taxa, mainly arthropods. However, most of these studies have focused on local patterns from a single desert or a transition zone between deserts rather than a region-wide analysis (Epps *et al.*, 1998; Smith and Farrell, 2005; Crews and Hedin, 2006). Ayoub and Riechert (2004) investigated phylogeographic patterns in a widespread desert-adapted spider, but, because the diversification of this species was linked to Pleistocene climatic cycles, the

patterns of divergence cannot be compared with the earlier Neogene diversification events found in the vertebrate taxa. In any case, little work on region-wide patterns has been conducted using arthropods. Before a generalized model of historical biogeography in the Nearctic deserts can be developed, investigations into the diversification of arid-adapted arthropods, which are more abundant and taxonomically diverse than any of the vertebrates, must be conducted and included in any consensus.

Likely arthropod candidates for investigating the biogeographic history of North America's deserts are arid-adapted groups within the wasp families Chyphotidae, Mutillidae and Tiphiidae (Hymenoptera). The nocturnal aculeate wasps are interesting from both evolutionary and biogeographical perspectives due to their great diversity and abundance in North American deserts (e.g., Schuster, 1958; Manley and Pitts, 2002; Wilson and Pitts, 2008). The geological and climatic events leading to the present-day diversity of nocturnal wasps, as well as other organisms in the deserts, remain somewhat controversial (Betancourt *et al.*, 1990; Klicka and Zink, 1997). Some authors have considered late Pleistocene glacial cycles of utmost importance (Findly, 1969; Hubbard, 1973; Tanner and Banta, 1977; Hewitt, 1996; Ibrahim *et al.*, 1996; Arbogast *et al.* 2001), while other authors suggest that different events, such as mountain orogeny and desert formation, are more important (Morafka, 1977; Riddle, 1995; Klicka and Zink, 1997; Orange *et al.*, 1999; Jaeger *et al.*, 2005). Clearly, the explanation of species diversity in the deserts cannot be ascribed arbitrarily to a single cause and these lineages should be useful for providing biogeographical information throughout the Neogene and Quaternary Periods.

Mutillidae are already known to be important for our understanding of the geological history of North America. Biogeographical analyses of nocturnal mutillids have produced interesting results and are helping to better establish the timing of key geological events in the southwestern United States (Pitts *et al.*, 2010b; Wilson & Pitts, 2010b, c; Wilson *et al.*, 2010, Wilson *et al.*, 2011). Most notably, both recent Pleistocene glaciation cycles and older orogenic events, albeit to a somewhat greater extent, were both causes of major diversification in nocturnal velvet ants (Pitts *et al.*, 2010b; Wilson & Pitts, 2010b), which is contrary to current ideas produced by mammalian and avian data. Additionally, specific phylogeographic analysis have shown that both late Neogene and early Pleistocene events were influential in the diversification of *Dilophotopsis* and the *Sphaeropthalma unicolor* (Cresson) species-complex, but Pleistocene climatic fluctuations seem to have been responsible for the split between the Mediterranean-adapted species and the desert-adapted species (Wilson & Pitts, 2009, 2010b, Wilson *et al.,* 2011).

The purpose of this study was to construct phylogenetic hypotheses for the nocturnal wasps of *Chyphotes* (Chyphotidae) and of *Brachycistis* (Tiphiidae) at the species level—the first for these groups of wasps—based on the phylogenomic approach that employs Ultra-Conserved Elements (UCE). Also, the purpose was to construct a more complete phylogeny of the nocturnal mutillid genus *Odontophotopsis* including additional taxa. In creating these phylogenetic hypotheses, molecular dating methods were employed to compare and determine the timing of key speciation events across all three groups linking them to known or hypothesized geological events, such as evidence

for the Baja Inner Peninsular Seaway. Additionally, these hypotheses will serve as a basis for a natural, higher-level classification and a framework for future comparative and biogeographical studies.

1.1 Taxonomic Background

Mutillids (Hymenoptera: Mutillidae), commonly known as velvet ants, are solitary, aculeate (stinging) wasps that are parasitic on other aculeate Hymenoptera, including bees (Apoidea) (Krombein, 1979; Nonveiller, 1990; Brothers, 1995), although a few species attack certain flies (Diptera) and beetles (Coleoptera) (Brothers, 1989). Many of the hosts are pollinators of ecological importance (Krombein, 1979). Historically, mutillids have been thought rare and to exist in low population densities. As this concept has been generally accepted in the literature, the rare occurrences of large numbers of individuals in an area are given special note (e.g., Manley and Taber, 1978; Schmidt and Hook, 1979; Polidori *et al.*, 2009).

Many species of mutillids are active primarily at night and these nocturnal species can be found in most desert regions of the world, except Australia. Of the three New World subfamilies of Mutillidae, Sphaeropthalminae contains all of the nocturnal Nearctic species, except for a single species of Mutillinae (*Timulla ocellaria* Mickel). The nocturnal Nearctic Sphaeropthalminae represent nearly half of the known Nearctic species and are classified into nine genera. Of special interest is the desert-adapted genus *Odontophotopsis* Viereck, which contains 49 species, and is restricted to the southwestern USA and northern Central America (Pitts *et al.,* 2010b). Morphological and

molecular data suggest its monophyly and split *Odontophotopsis* into two clades, each containing taxa distributed among the North American arid zones (Pitts *et al.,* 2010b). The highest diversity of *Odontophotopsis* species is in the Sonoran desert, but a diverse fauna also exists in other deserts and surrounding arid lands. Because this genus is found throughout North America's arid lands, and individual species are isolated in specific regions, it is an ideal candidate to examine historical biogeography of the Nearctic arid regions.

Members of Chyphotidae are also potentially important for our understanding of the geological history of North America due to the high-level of endemism in arid regions. This family is comprised of two subfamilies Chyphotinae and Typhoctinae (Pilgrim *et al.*, 2008, Branstetter *et al.,* 2017). While Typhoctinae is found throughout the New World, Chyphotinae is only found in the western Nearctic region. Chyphotinae has only one genus, *Chyphotes*, and two subgenera, *Chyphotes* and *Pitanta*. Although the genus currently has 54 described species, the actual number is much lower. Forty-eight of the 54 species are known from a single sex, but, based on male morphology, the genus likely contains only 34 species, all of which are nocturnal and desert-adapted (Mickel, 1967; Mickel, 1974). Most species are abundant, and the genus can be found from Southern Canada to Northern Mexico with the majority of species occurring in the southwestern United States. It has been speculated that one member of Chyphotidae (*Typhoctes pecularis* Cresson) uses camel spiders (Arachnida: Solifugae) as a host (Brothers, 1995). This claim remains unsubstantiated, and due to the nature of both solpugids and Chyphotidae seems highly unlikely. Currently, the hosts of these two

groups of solitary nocturnal wasps remain unknown, but are likely Scarabaeidae, Tenebrionidae, or Carabidae beetles (Coleoptera) based on evolutionary relationships (e.g., Pilgrim *et al.*, 2008, Branstetter *et al.,* 2017). Females are solitary, wingless, and strictly nocturnal, are well adapted to subterranean lifestyles, and seem to have limited dispersal capability. All of these factors make females elusive not only for collection, but also for the study of host use and other biological processes.

Tiphiidae also has many species that are endemic to specific Nearctic arid regions making them possible candidates for historical biogeography. Tiphiidae is comprised of two subfamilies Brachycistidinae and Tiphiinae (Pilgrim *et al.,* 2008, Branstetter *et al.,* 2017). While Tiphiinae is cosmopolitan and typically diurnal, Brachycistidinae is restricted to the western Nearctic venturing as far south as Costa Rica and contains mostly nocturnal desert-adapted species (Pilgrim *et al.*, 2008, Branstetter *et al.,* 2017). Brachycistidinae has 12 genera (*Acanthetropis*, *Brachycistellus*, *Brachycistina*, *Brachycistis*, *Brachymaya*, *Colocistis*, *Dolichetropis*, *Glyptacros, Hadrocistis, Paraquemaya*, *Sedomaya,* and *Stilbopogon*) and a total of 77 species, most of which are desert adapted (Kimsey and Wasbauer, 2006). *Brachycistis* is the largest of the genera with 28 species. Males are collected in much higher numbers, resulting in a taxonomy relying heavily on one sex. With the exception of the three largest genera (*Brachycistis*, *Stilbopogon*, and *Colocistis*), most genera are known from a single sex. Females have been placed into genera without being associated with any male. As is true of other nocturnal aculeate wasps, females are exceptionally rare and associations are difficult.

Due to the lack of specimens, and difficulty of capture, their natural history remains unknown.

2. Materials and methods

2.1 Collecting methods

Fresh specimens of nocturnal wasps were collected for molecular work throughout the southwestern US during the summers of 2005–2016. Nocturnal wasps were collected at >80 field sites, yielding >100,000 specimens. Specimens were collected using black-light traps, fluorescent lantern traps, and by hand. Specimens collected with light traps were captured in soapy water and transferred into 95% ethanol, while all hand-collected specimens were placed directly into 95% ethanol.

2.2 Ingroup selection

Taxon sampling strategy is an important component of phylogenetic analyses, because outcomes are often sensitive to the number and identity of taxa (Lecointre *et al.*, 1993; Sanderson, 1995; Graybeal, 1998; Hillis, 1998; Zwickl and Hillis, 2002). For *Chyphotes*, we included 34 described species and 7 undescribed species out of a possible 37 described species, of which 19 described species and 5 undescribed species were from *Pitanta,* and 15 described species and 2 undescribed species were from the nominal subgenus. For *Brachycistis,* we included 14 representatives out of a possible 28 species. These *Brachycistis* species included one of five species from the *nitida* species-group, two of seven from the *petiolata* species-group and 11 of 16 from the *ampla* species-

group. For *Odontophotopsis,* we included 40 described species and 8 undescribed species out of a possible 49 species. This increased the number of species by 11 from Pitts *et al.* (2010). We also were able to include members of the *Odontophotopsis dentifera* and *O. serca* species-groups occurring in Baja California, Mexico, which enabled us to investigate patterns of diversification across more North American deserts than was previously possible.

2.3 Outgroup selection

For *Chyphotes,* outgroups were chosen from Typhoctinae, which is the only other subfamily in Chyphotidae, and included eight species from the genera *Eotilla*, *Prototilla*, and *Typhoctes*. This includes eight of the 12 species in Typhoctinae. Five further outgroups were chosen from Tiphiidae and Thynnidae. For *Brachycistis,* outgroups were chosen from Chyphotidae and also from Tiphiinae, which is the only other subfamily in Tiphiidae, and included two species. For *Odontophotopsis,* outgroups were chosen due to their morphological similarity to the ingroup taxa based on Pitts *et al.* (2010). Individuals from seven species of other closely related nocturnal genera, including *Acrophotopsis* Schuster, *Dilophotopsis* Schuster, *Laminatilla* Pitts, and *Sphaeropthalma,* were included as more distant outgroups. Individuals of *Pseudomethoca* and *Dasymutilla* were used as even more distant outgroups, which was especially advantageous given that two *Dasymutilla* species are described from Dominican amber fossils.

2.4 DNA isolation, amplification, and sequencing

DNA was extracted from ethanol-preserved specimens, as well as recently collected pinned, dried specimens using the High Pure PCR Template Preparation Kit (Roche Pharmaceuticals, Indianapolis, IN). DNA was extracted from the entire individual by either piercing the thorax or removing a pair of legs so the extraction solutions could penetrate the specimen. This process preserved the external anatomy of the individual for identification. Voucher specimens were deposited in the Department of Biology Insect Collection (EMUS), Utah State University, Logan, UT.

For *Odontophotopsis*, the two internal transcribed spacers (ITS1 and ITS2) of the nuclear ribosomal RNA cistron were sequenced for representatives of each species. PCR was used to amplify the ITS1 and ITS2 regions using the molecular protocols described in Pilgrim and Pitts (2006). Gel electrophoresis of each intergenic region yielded a single band for each individual wasp and the resulting sequences exhibited no polymorphism, suggesting there were no problems with heterogeneity as seen in some other organisms (e.g., Harris and Crandall, 2000; Parkin and Butlin, 2004; Bower *et al.*, 2008). Each PCR product was sequenced in both directions and the two reads assembled using Geneious R9 v9.0.2 (Kearse et al., 2012). Although microsatellite insertions can be common in the rDNA transcribed spacer regions (e.g., Fairley *et al.*, 2005), assembled sequences showed no indication of problems that can be associated with these types of insertions. Corrected sequences from all samples were aligned separately for ITS1 and ITS2 using the default parameters in ClustalW (Thompson *et al.*, 1994). Alignments were visually inspected and noted errors were corrected in Geneious R9 v9.0.2 (Kearse et al., 2012). The alignment

contained areas that were highly conserved across all taxa and other areas that had many insertions and deletion polymorphisms (indels). These less conserved areas did, however, contain phylogenetic informative sites and were conserved within groups deemed closely related based on morphology. While all of the taxa had indels, which is not unexpected given the non-coding nature of these intergenic regions, the alignment was informative. Because both the highly conserved regions and the less conserved regions contained informative sites, we included the entire alignment in the phylogenetic analyses rather than excluding the less conserved areas. All sequences were deposited in GenBank.

For *Chyphotes* and *Brachycistis*, a novel sequence capture method was employed that takes advantage of Ultra Conserved Elements (UCE), which are short stretches of highly conserved DNA found in many organisms (Siepel *et al.,* 2005; Faircloth *et al.,* 2012). These conserved stretches are accompanied by DNA flanking either side with enough variation to produce phylogenetic signal at both family and species level (Faircloth *et al.,* 2012, 2015; Faircloth, 2013; McCormack *et al.,* 2012; Jarvis *et al.,* 2014). UCE data can easily be obtained from samples previously collected for traditional molecular work or even from dried museum specimens (Blaimer *et al.*, 2016), negating the demands for specific preservation protocols that other genomic approaches, such as full genome or transcriptome sequencing may require.

The methods were derived from those of Faircloth *et al.* (2012), Branstetter *et al.* (2016, 2017) and that of others (Rohland & Reich, 2012). Faircloth and Branstetter have developed specialized probe kits that have shown high success with our target taxa in preliminary studies (Faircloth *et al.,* 2015, Branstetter *et al*. 2017). First, DNA was

extracted and mechanically sheared to a length of ~600bp. DNA libraries were generated to be used with a specialized Tru-seq style dual indexing adapter system allowing for multiplexing and hybridization to enrich libraries. Quantification of adapter-ligated fragments post enrichment will was performed via quantitative Polymer Chain Reaction (qPCR) to ensure capture of UCE loci. Due to the short fragment size, and specialized indexing system allowing each individual to be uniquely tagged, libraries were pooled. A library of all individuals was combined into one pool and submitted to one lane on an Illumina sequencer at the University of Utah.

2.5 Model selection and analyses

The data sets of the two intergenic regions were analyzed with jModeltest v2.1.4 (Dariba *et al*., 2012; Guindon and Gascuel, 2003) to determine the appropriate models for Bayesian analysis. These regions were then subjected to Bayesian analysis individually and as a combined data set, with each region partitioned according to its appropriate model and with all parameters unlinked across regions. All Bayesian analyses for *Odontophotopsis* were run with MrBayes v3.2.5 (Ronquist *et al.,* 2012) and included four independent runs with three heated chains and one cold chain in each run. The MCMC chains were set for 20,000,000 generations and sampled every 1000 generations; chains were run until the average standard deviation of the split frequencies dropped below 0.01. A burnin of 20,000 samples was removed after graphical determination of stationarity.

For *Chyphotes* and *Brachycistis*, sequencing data was analyzed using the PHYLUCE v 1.5 package (Faircloth, 2015). Illumiprocessor was used to clean reads

while assemblies were made *de novo* using Trinity v r2013-02-25. PHYLUCE was also used to search for reads matching the UCE loci from the RNA bait library; this process removed reads that caused difficulties for assembly, were duplicates, or did not closely match the targeted loci (Faircloth *et al.,* 2012). The aligned dataset was generated using MAFFT v7.130b and trimmed using Gblocks v0.91b. Finally, PHYLUCE was used to filter the set of trimmed alignments resulting in a dataset that contained 90% of the taxon sampled; this was true for both *Chyphotes* and *Brachycistis*.

Maximum likelihood trees were inferred from concatenated matrices in RAxML v8 using 100 rapid bootstrap replicates. The data was partitioned by UCE loci and the model of evolution was set to the General Time Reversible model with gamma distributed rate variation among sites (GTR+ Γ).

2.6 BEAST analysis

The program BEAST uses the aligned sequence data to generate a tree and estimate divergence dates. We used the program BEAUti v. 1.8.4 (Drummond *et al.*, 2012) to prepare the file for BEAST using the combined sequence data from both ITS1 and ITS2. For *Odontophotopsis*, we constrained the node at the base of the *Dasymutilla* clade by making a taxon set which included only the *Dasymutilla* species, and giving this taxon set a normally distributed prior with a mean age of 20 Ma with a standard deviation of 1.0. We applied a normally distributed prior to the root node with a mean age of 65 Ma with a standard deviation of 15 Ma, because the tribe cannot be older than the family Mutillidae, which likely originated around this time (Grimaldi and Engel, 2005). These

dates are secondary calibration points as determined by Pitts *et al.* 2010, in which Dasymutilla fossils were used to determine age estimates for nocturnal mutillids.

Neither *Chyphotes* nor *Brachycistis* have known fossils, so calibration for these groups were based on dates determined in Wilson *et al.* (2013). Considering our analyses were from secondary calibration points, we used a standard deviation of 15 Ma for all dates to ensure conservative estimates¸ and all priors were normally distributed. For *Chyphotes*, we constrained the node at the base of the subfamily, Chyphotinae, to have a mean age of 37 Ma, and a mean age of 35 Ma was set for Typhoctinae. The entire family was set to 90 Ma, and the root node to 97 Ma. For *Brachycistis,* the root node was set to 97 Ma, for the non-*Brachycistis* ingroup a date of 30 Ma was set, and Tiphiidae was set to 73 Ma.

With datasets as large as 1,000,000 base pairs, we decided to use a reduced dataset that only included the 100 most informative loci to significantly reduce computational time. With bootstrap values of 100 for almost all nodes, the RAxML trees were used as constraint trees to further reduce computation time. The relaxed molecular clock was set to an uncorrelated lognormal model. For *Chyphotes* three independent runs were made at 150 million generations each, for *Brachycistis* four independent runs were made set to 100 million generations each, and two runs of 60 million generations each for *Odontophotopsis.* Runs for each group were then combined using LogCombiner v1.8.4 (Drummond *et al.*, 2012). Convergence and burnin were assessed using Tracer v1.5 (Rambaut and Drummond, 2007), and implemented in TreeAnnotator v1.8.4. (Drummond *et al.*, 2012).

2.7 Ancestral Area Reconstruction

For biogeographical analyses, ancestral areas were inferred using the software RASP (Reconstruct Ancestral State in Phylogenies)**.** For biogeographical analyses, species were categorized into 14 areas (A = Sonoran Desert, west; B = Sonoran Desert, east; C = Mojave Desert; D = Great Basin Desert; E = Madrean Archipelago; F = Chihuahuan Desert; G = Colorado Plateau; H = Southern Baja Desert, Mexico; I = Great Plains; J = Arid regions of Mexico, including Sinaloa and southward; K = Central Valley of California; L = arid regions north of the Great Basin Desert; M = Australia; and N= South America) based on geographical distributions obtained from the Department of Biology Insect Collection at Utah State University and Chapters 3, and 4. The ancestral areas and biogeographical history of these nocturnal wasps were inferred using the software RASP 3.02 (Yu *et al.*, 2015)**.** A Bayesian binary MCMC method was used for the ancestral reconstruction using the most general and complex of the models in RASP, model F81+Γ. The MCMC chains were run for 10 million generations and sampled every 1000 generations. The first 1000 were removed as burn-in.

3. Results

3.1 Alignments and best-fit models

For *Odontophotopsis*, a total of 48 nocturnal species and 10 outgroup species were included in the phylogenetic analysis. The final alignment encompassed 2,273 base pairs. The best-fit model for each intergenic region resulting from jModeltest was the general time-reversible model (Lanave *et al.*, 1984) with gamma-distributed rate variation

across sites (GTR + Γ). Although some sequence length variability was present in the data set, which introduced gaps into the alignment, gaps were treated as missing data in MrBayes, and, therefore, did not contribute to the phylogenetic hypothesis.

For *Chyphotes*, a total of 41 nocturnal species and 13 outgroup species were included in the phylogenetic analysis. The final alignment for UCEs contained 1,046 loci totaling 1,008,723 base pairs of which 497,610 were informative sites.

For *Brachycistis*, a total of 19 nocturnal species and 18 outgroup species were included in the phylogenetic analysis. For *Brachycistis* the final alignment for UCEs contained 816 loci totaling 690,178 base pairs of which 256,767 were informative sites.

3.2 RAxML analyses

For *Chyphotes,* ML analysis of the UCE data produced a well-resolved tree with only two nodes with bootstrap values less than 100 (Fig. 5.1). *Chyphotes* species were placed into two major clades which represent the current subgeneric classification of the two subgenera, *Chyphotes* and *Pitanta.*

For *Brachycistis,* ML analysis of the UCE data produced a well-resolved tree with no nodes with bootstrap values less than 100 (Fig. 5.2). *Brachycistis* species were placed into four major clades and do not reflect the current three species-group classification of Wasbauer (1966).

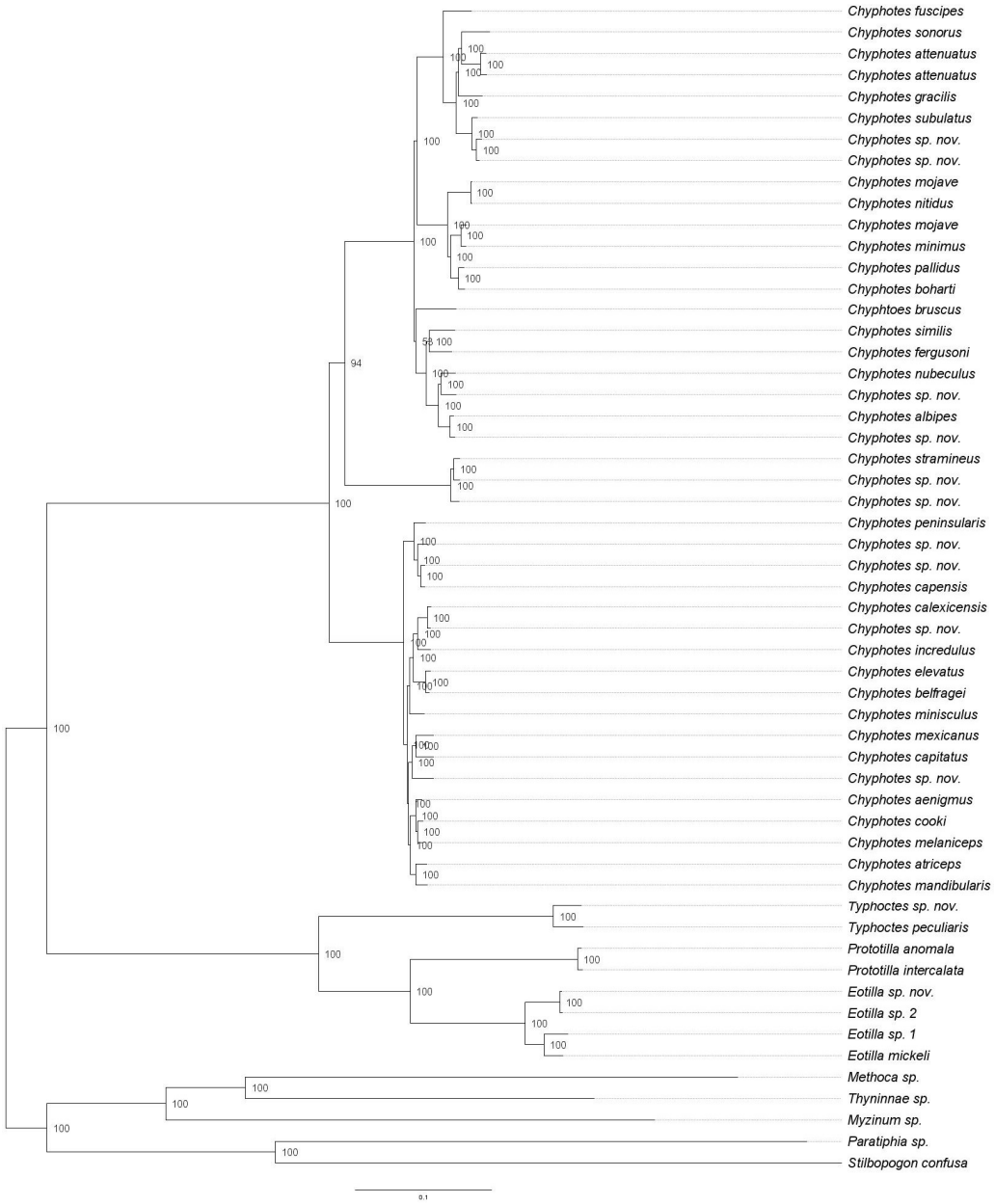

Fig. 5.1. Maximum likelihood tree based on ultra-conserved element data of *Chyphotes* in RAxML. Node numbers indicate maximum-likelihood bootstrap support values.

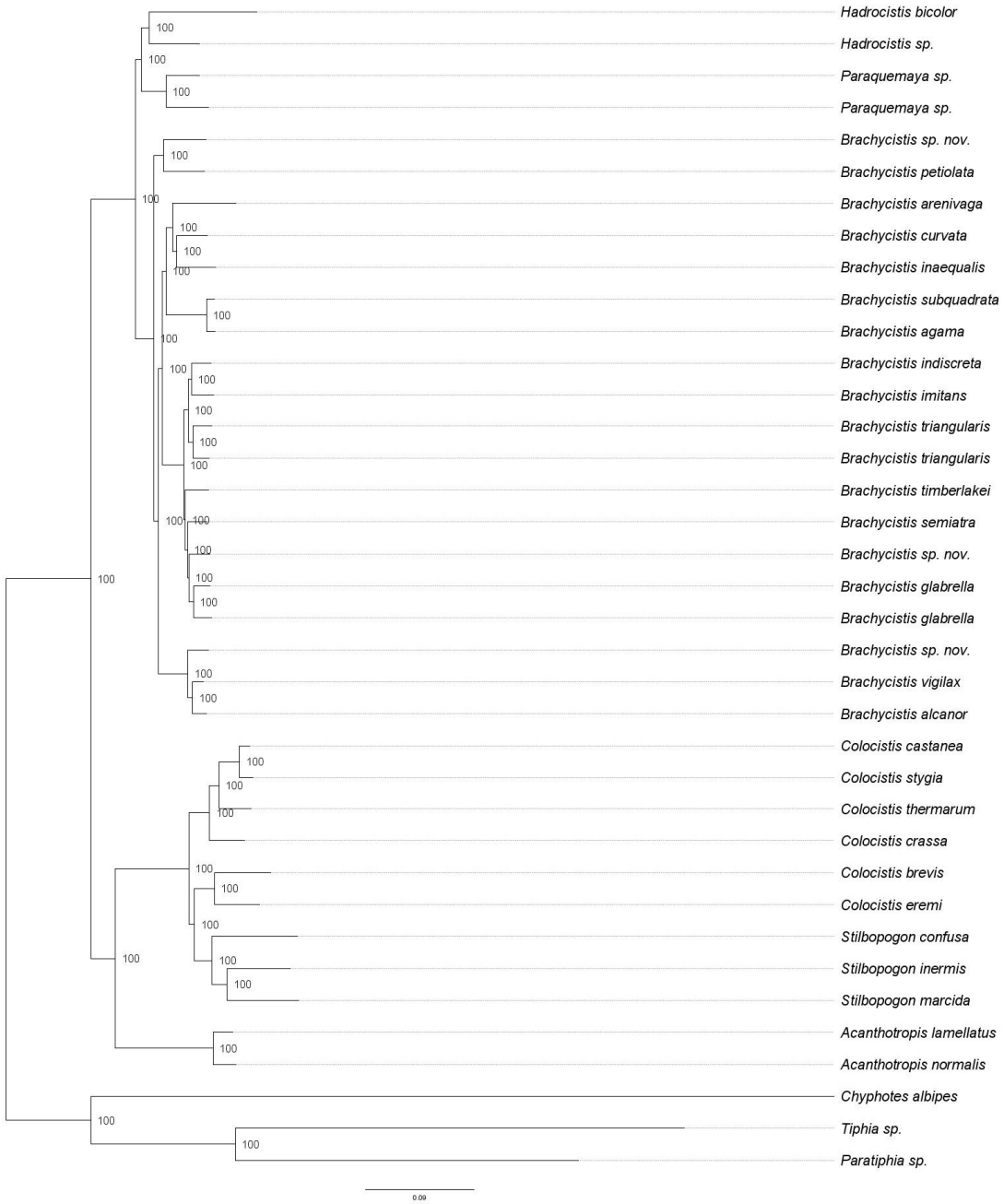

Fig. 5.2. Maximum likelihood tree based on ultra-conserved element data of *Brachycistis* in RAxML. Node numbers indicate maximum-likelihood bootstrap support values.

3.3 Bayesian analyses

For *Odontophotopsis,* Bayesian analyses of the two ITS intergenic regions analyzed individually produced trees with lower overall resolution than the combined data set, and are not shown. Both intergenic regions strongly supported the monophyly of the *Odontophotopsis*. Ingroup relationships within the consensus tree for each intergenic region were similar, but the levels of posterior probability (PP) support in the consensus trees were different. ITS1 data produced a well-resolved tree with high posterior probabilities (>0.95) for most nodes including all but two of the backbone nodes. Bayesian analysis of the ITS2 data produced a less well-resolved tree than ITS1, with high PPs (>0.95) for most terminal nodes, but with lower PPs (<0.95) for the backbone nodes. Otherwise, relationships of the major lineages were the same as those derived from ITS1 data. Bayesian analysis of the combined ITS data produced a tree with well-resolved ingroup relationships, which had higher posterior probabilities than either single-intergenic region analysis; PPs were >0.95 for most nodes (Fig. 5.3). *Odontophotopsis* species were placed into four major clades not differing much from Pitts *et al.* (2010).

3.4 Molecular dating

Results from the BEAST analysis for *Chyphotes*, *Brachycistis*, and *Odontophotopsis* are shown Figs. 5.4, 5.5, 5.6. Percentages of species evolving prior to the Neogene, during the Neogene and afterwards in the Pleistocene are compiled in Table 5.1. Dating analyses suggested the majority of extant nocturnal (62 spp.) species

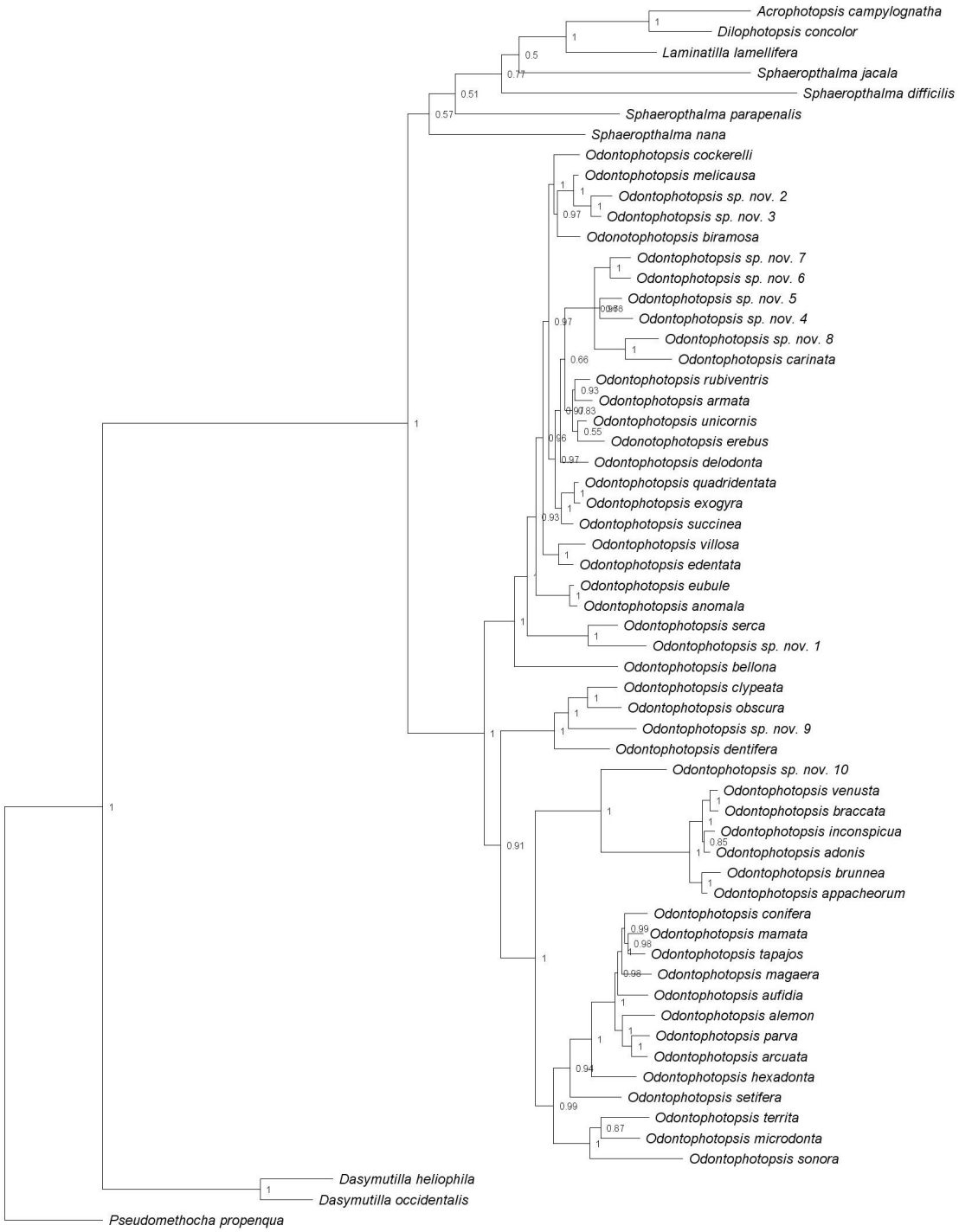

Fig. 5.3. Post-burnin 95% consensus tree from the Bayesian analysis of the combined molecular data set of ITS1 and 2 for *Odontophotopsis*. Numbers at each node represent the posterior probabilities.

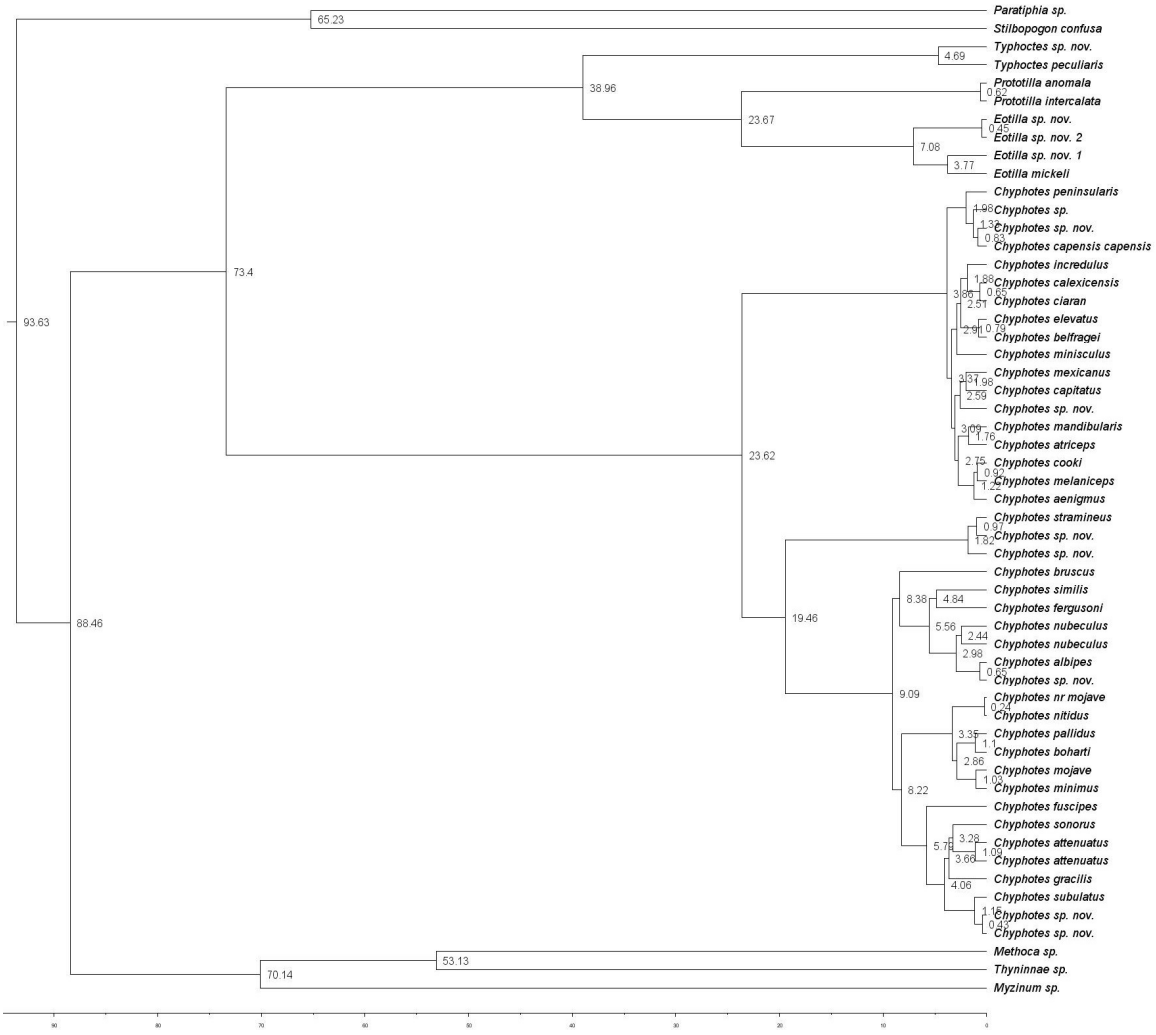

Fig. 5.4. Bayesian inference of based on ultra-conserved element data for *Chyphotes* in BEAST 1.8.0. Node numbers indicate the mean estimated divergences times in millions of years.

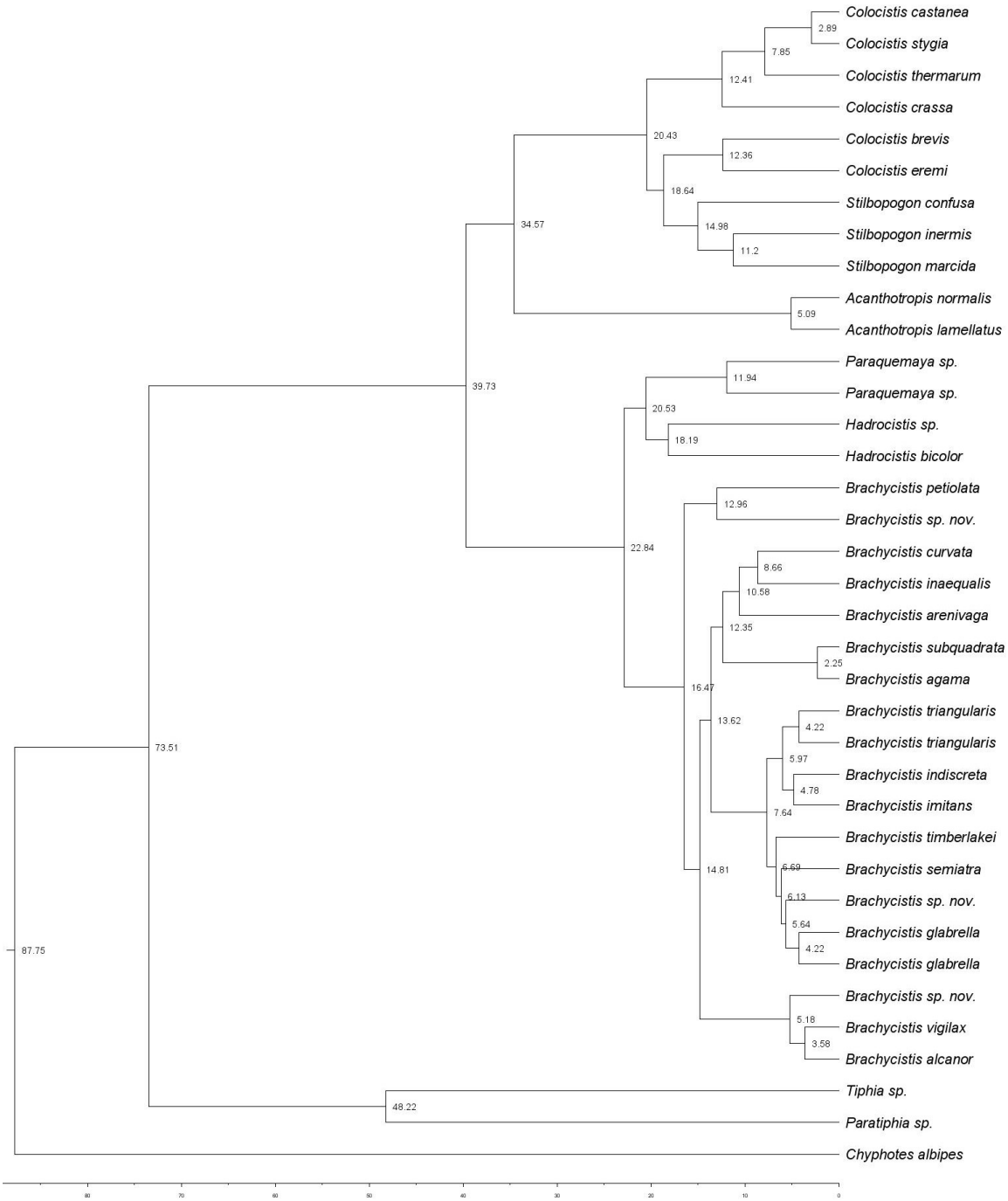

Fig. 5.5. Bayesian inference of based on ultra-conserved element data for *Brachycistis* in BEAST 1.8.0. Node numbers indicate the mean estimated divergences times in millions of years.

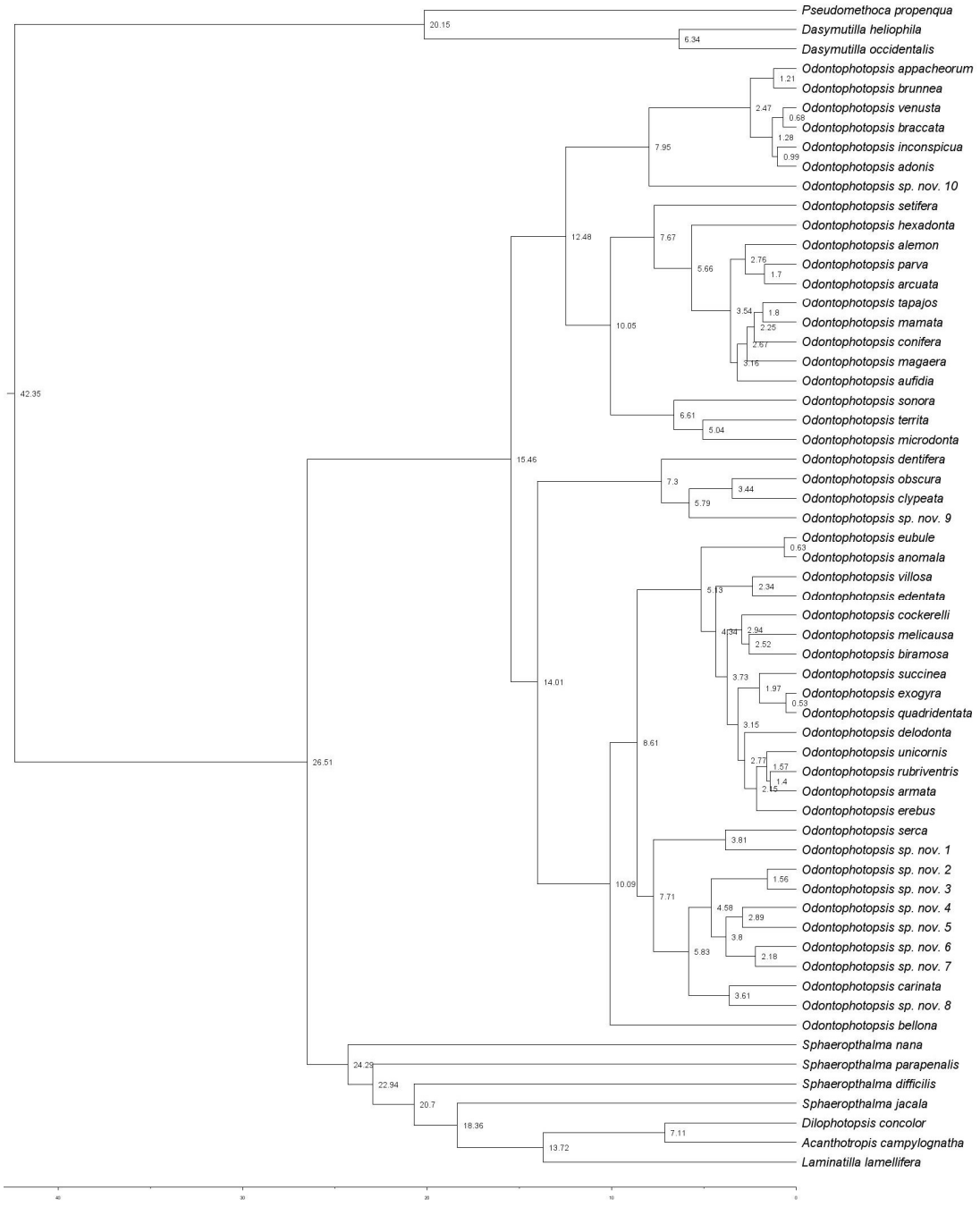

Fig. 5.6. Bayesian inference of the combined molecular data set of ITS 1 and 2 for *Odontophotopsis* in BEAST 1.8.0. Node numbers indicate the mean estimated divergences times in millions of years.

Table 5.1
Percentage of ingroup species evolving prior to the Neogene, during the Neogene and during the Pleistocene based on Bayesian inference as implemented in BEAST based on a Dominican amber fossil age of 20 Ma.

	Species evolving before Neogene (%)	**Species evolving in Neogene (%)**	**Species evolving in the Pleistocene (%)**
Odontophotopsis	0	63	37
Chyphotes	0	31	69
Brachycistis	0	100	0

originated between 15 Ma and 1.8 Ma in the Neogene, while none evolved before the Neogene and 48 spp. evolved during the Pleistocene. *Brachycistis* had the highest proportion of species originating the Neogene (100%), while *Chyphotes* had the lowest (31%). Conversely, *Brachycistis* had no species evolving during the Pleistocene, while *Chyphotes* has the most with 69% evolving during this time. *Odontophotopsis* had values in between for the two geological periods. For all analyses the confidence intervals around each node were larger for the deeper nodes and smaller for the nodes near the tips of the tree. RASP analyses are given in figures 5.7, 5.8, and 5.9.

4. Discussion

4.1 Impact of Neogene orogeny and Pleistocene glaciation on speciation

Two major abiotic influences are thought to have caused diversification of Nearctic desert biota, with one older event beginning in the middle Miocene and a more recent

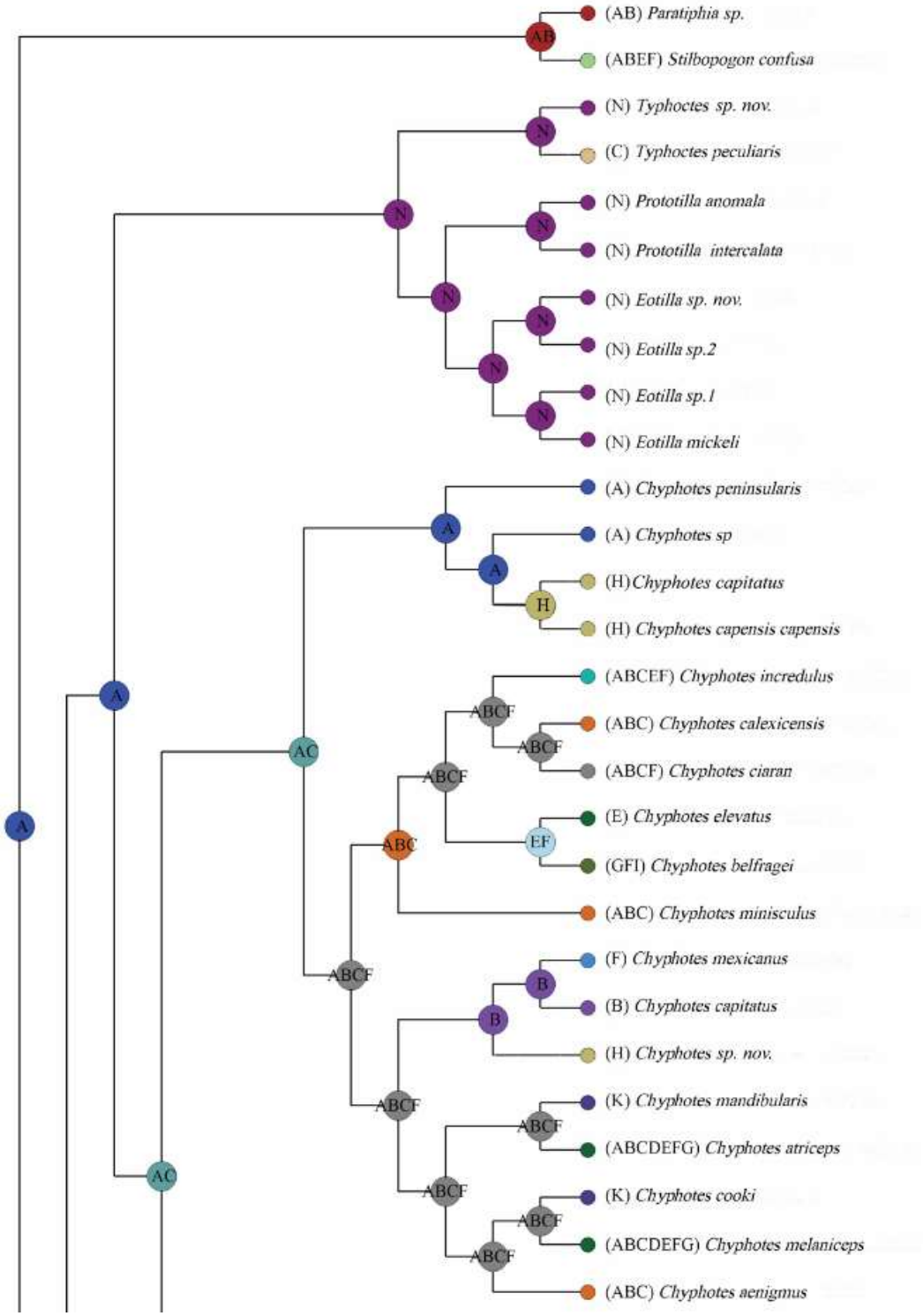

Fig. 5.7. Ancestral-area reconstruction of *Chyphotes* using RASP 3.02.

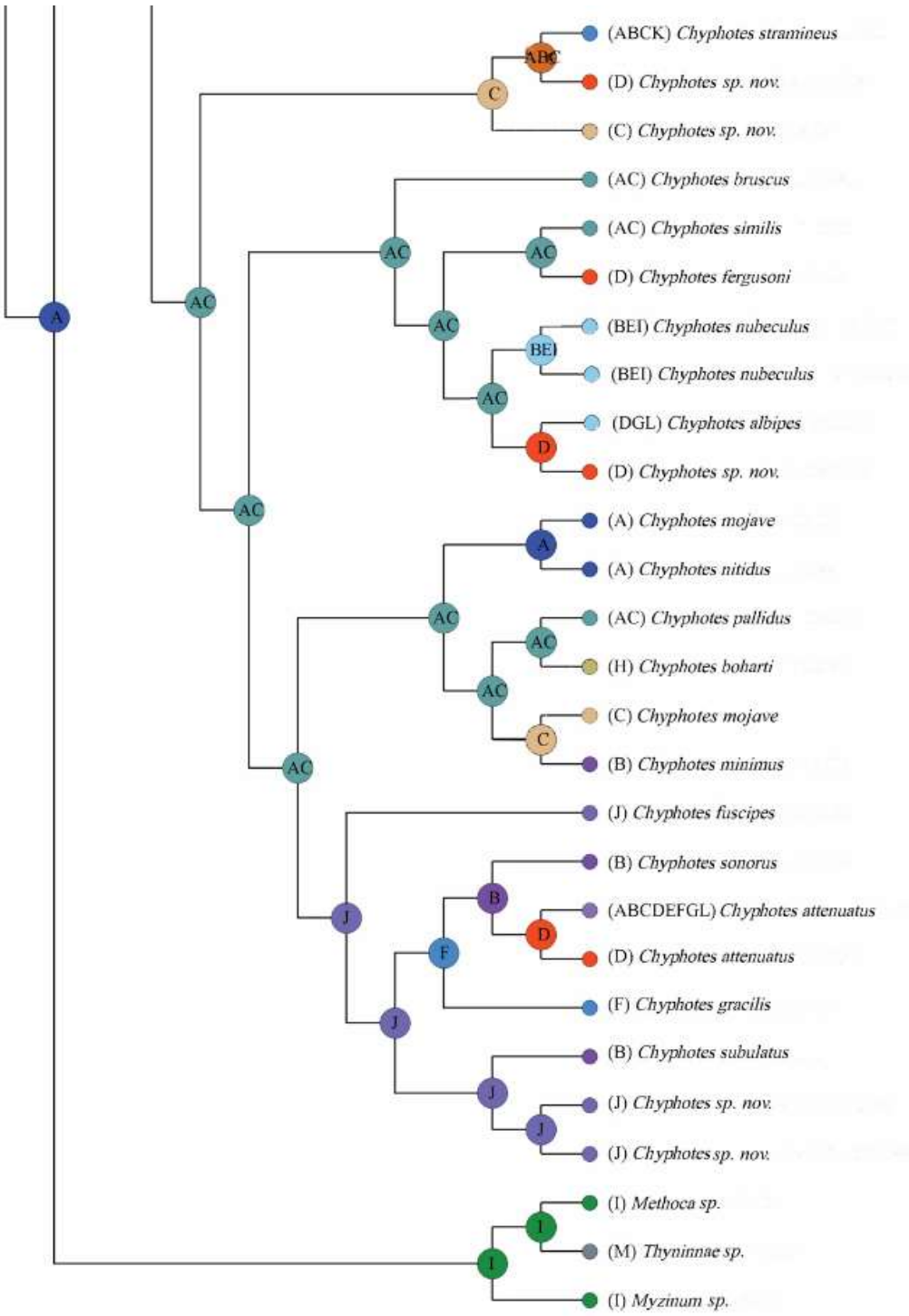

Fig. 5.7. Continued.

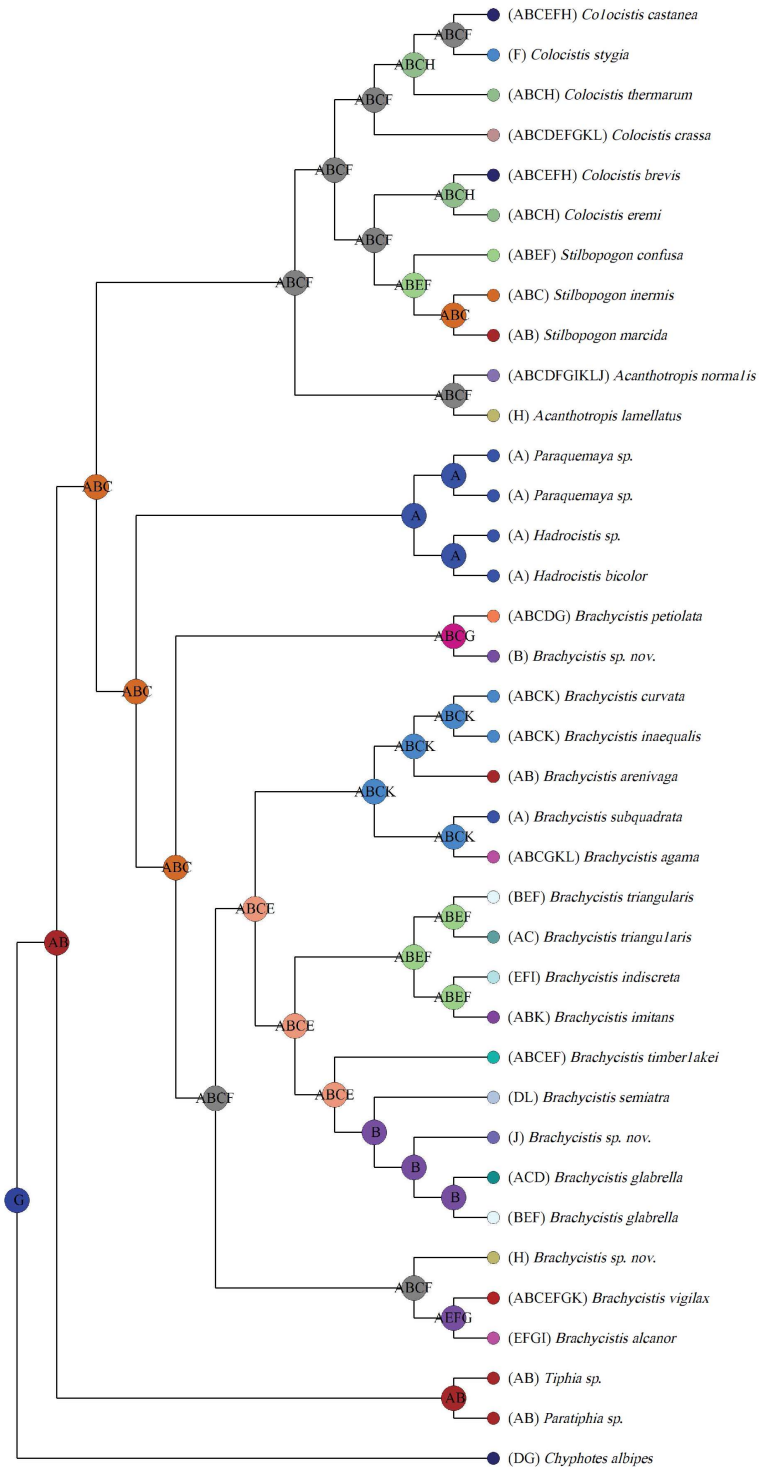

Fig. 5.8. Ancestral-area reconstruction of *Brachycistis* using RASP 3.02.

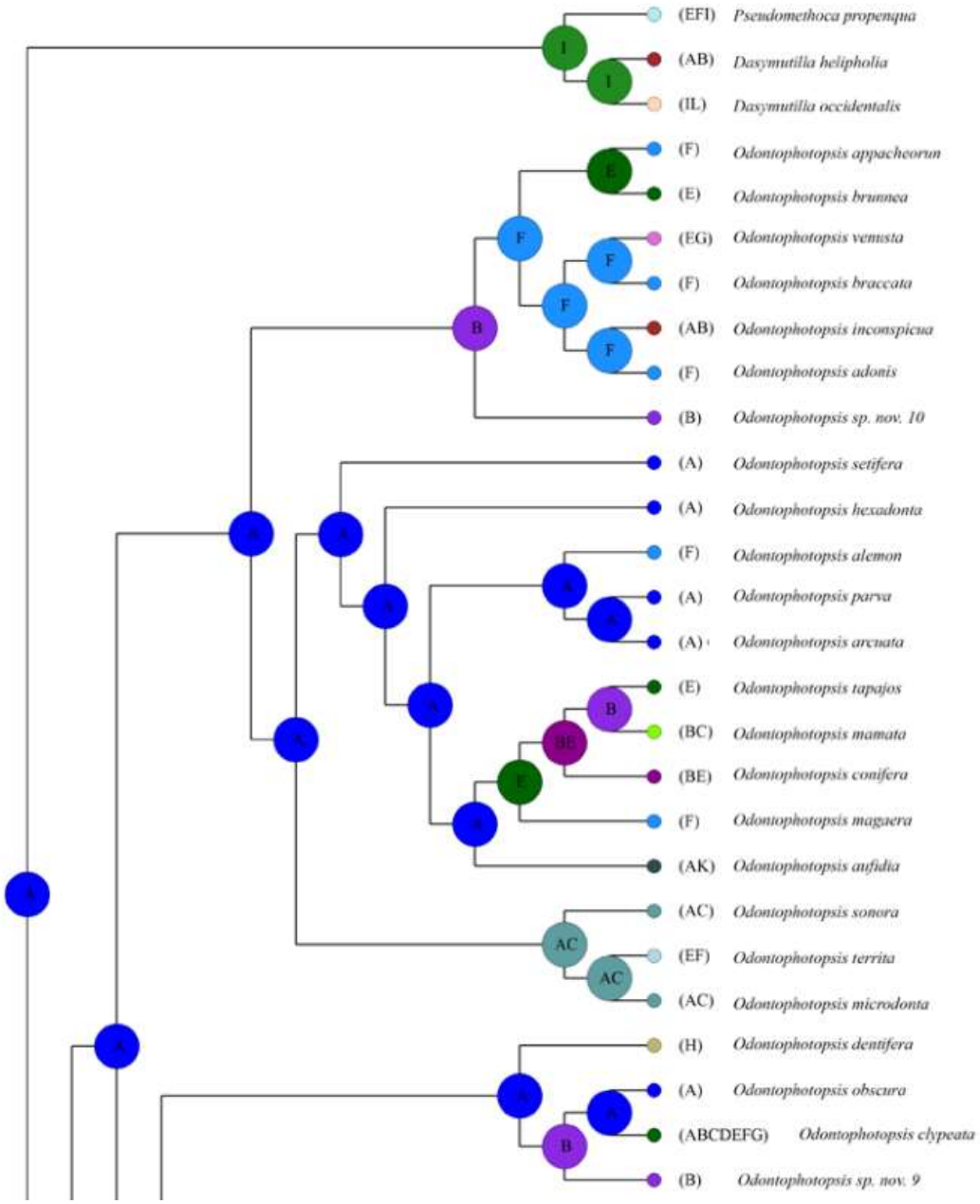

Fig. 5.9. Ancestral-area reconstruction of *Odontophotopsis* using RASP 3.02.

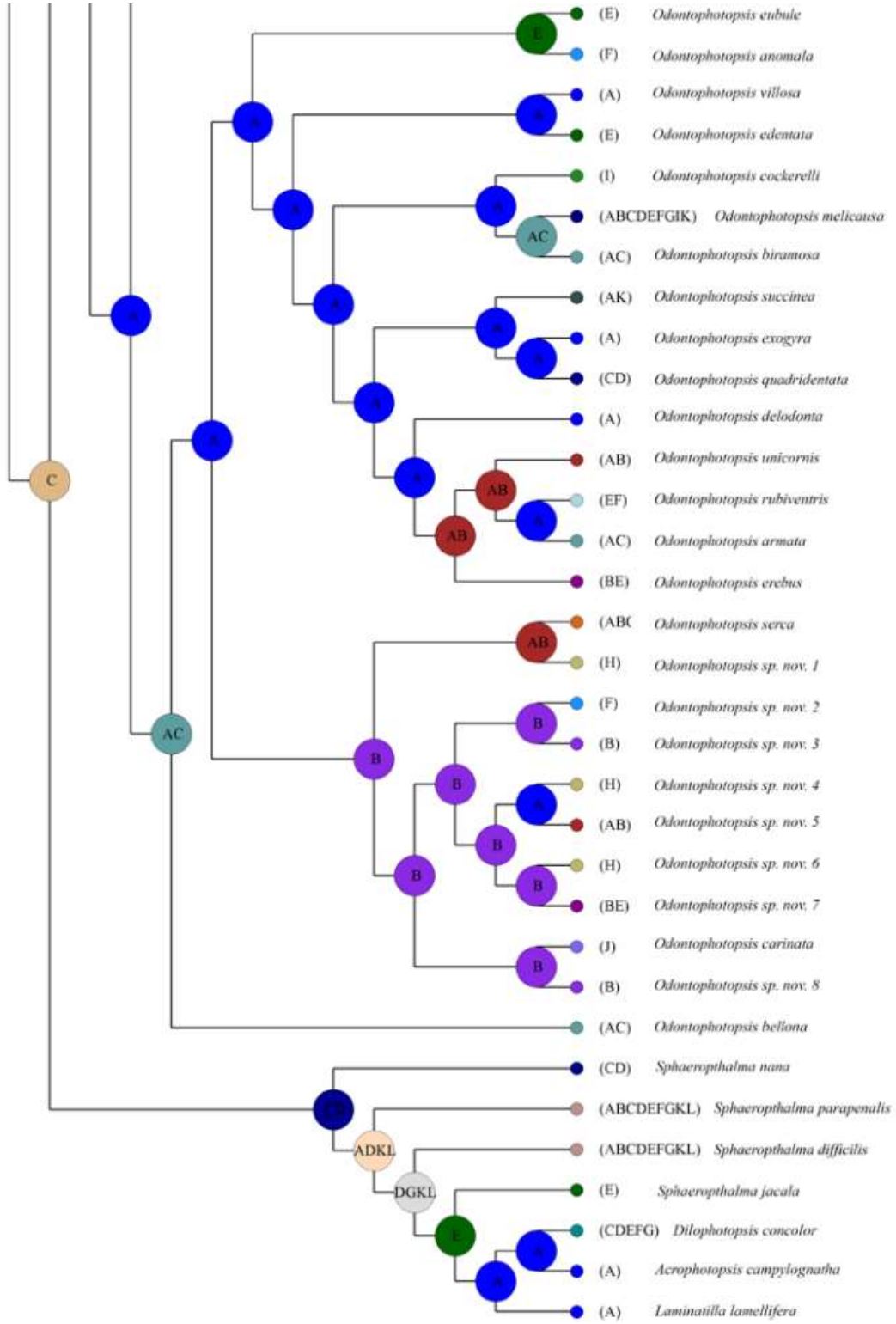

Fig. 5.9. Continued.

event in the Quaternary period. The scientific literature suggests that the older Miocene orogenic processes, namely uplift of the western North American mountain ranges (the North American Cordillera), was a major driving force for some groups (e.g., Morafka, 1977; Riddle, 1995; Klicka and Zink, 1997; Orange *et al.*, 1999; Jaeger *et al.*, 2005). Diversification in several western North American taxa has been attributed to Neogene mountain uplift events, including reptiles and amphibians (Tan and Wake, 1995; Shaffer *et al.*, 2004; Jaeger *et al.*, 2005; Devitt, 2006; Douglas *et al.*, 2006), as well as rodents (Riddle, 1995) and plants (Moore and Jansen, 2006). While some of these taxa are widespread, and were likely acted on by the uplift of different mountain ranges (e.g., mice, Lyre snakes, and toads), others are restricted in distribution and likely were affected just by the uplift of the Sierra Nevada (e.g., newts and salamanders). Regrettably, there is much uncertainty associated with the timing of mountain uplift in western North America (Wilson and Pitts, 2010) making it difficult to determine which uplift events contributed to diversification. Because of discrepancies in the dates given for the mountain uplift with some authors suggesting the majority of uplift occurred in the middle Miocene (15 Ma) (e.g. Hay and Soeding, 2002) and others suggesting that it was as recent as the late Pliocene (1.8 Ma) (e.g. Clark *et al.*, 2005), Wilson and Pitts (2010) have proposed that any speciation events dated between approximately 15 Ma and 1.8 Ma could reasonably be linked to mountain building events, while speciation events more recent than 1.8 Ma were likely caused by climate change in the Pleistocene. Our analyses show that both Neogene orogeny and Pleistocene glaciation have impacted speciation in the nocturnal wasps. Two further general conclusions can be drawn from

these analyses. First, the dates inferred for speciation events suggest that Neogene orogeny was more influential than Pleistocene climatic cycles in diversification of *Brachycistis* and *Odontophotopsis*. This conclusion was also arrived at by Pitts *et al.* (2010) for other nocturnal velvet ants. Second, Pleistocene-age speciation events, although less numerous than those occurring in the Neogene for *Odontophotopsis*, constitute a moderate to large proportion of the overall events and should not be trivialized. For *Chyphotes,* a major proportion of species evolved in the Pleistocene. Pleistocene-age speciation events could be rarer than Neogene speciation in *Brachycistis* and *Odontophotopsis* due to incomplete isolation in some species. Other reasons for the rarity of speciation events in the Pleistocene could be that any incipient species could have been erased by re-mixing during interglacial cycles, especially due to the large population sizes of these wasps compared to that of *Chyphotes*, or the time-span was insufficient for speciation to occur (Pitts *et al.* 2010).

Concerning the evolution of nocturnal behavior in these groups, our dating analyses suggest that the ancestors to each of these taxa may have been already nocturnal before the deserts formed based on currently accepted dates (e.g. Wilson and Pitts, 2010). Nocturnal behavior likely evolved between 73 and 24 Mya for *Chyphotes,* 74 and 40 Mya for *Brachycistis,* and 27 to 15 Mya for *Odontophotopsis,* which is older that most ages given for the Southwestern deserts (Wilson and Pitts, 2010). This conclusion was also arrived at by Pitts *et al.* (2010) for other nocturnal velvet ants. However, nocturnality evolving as a response to increased aridity or desert formation cannot be ruled out.

For those species of *Chyphotes* and *Odontophotopsis* that have recently speciated (<1 Ma), these events are consistent with a hypothesis of past fragmentation of habitats by glacial cycles during the Pleistocene, and subsequent range expansion. Several species pairs in the phylogeny suggest an event that fragmented ancestral populations between the Chihuahuan and Sonoran deserts during the Pleistocene occurred at the Deming Plains. The dates range between 4.78 Mya and 0.63 Mya with an average of 1.58 Mya. Specific dates and species pairs for this event are 4.78 Mya (*B. indescreta* and *B. imitans*) from *Brachycistis,* 1.98 Mya (*C. capitatus* and *C. mexicanus*) and 0.79 Mya (*C. belfragei* and *C. elevatus*) for *Chyphotes* species, and 1.8 Mya (*O. mamata* and *O. tapajos*), 1.4 Mya (*O. armata* and *O. rubriventris*), 1.21 Mya (*O. appacheorum* and *O. brunnea*), 0.99 Mya (*O. adonis* and *O. inconspicua*), 0.68 Mya (*O. braccata* and *O. venusta*) and 0.63 Mya (*O. anomala* and *O. eubule*) for *Odontophotopsis*.

These data presented here can also be specifically used to address dates specific to the Boues Sea Embayment and to the hypothesized Baja Inner Peninsular Seaway, as well as its validity. A model based on the underlying historical assembly of herpetofauna of the Baja Peninsular Desert has been developed predicting that three geological events followed the initial formation of the Gulf of California and Sea of Cortéz 5.5 Mya, but came before the major climatic cycles of the Pleistocene (Murphy 1983a,b; Grismer 1994; Upton and Murphy 1997). The first event was that the Sea of Cortéz extended inland as far north as the San Gorgonio Pass in southern California forming the San Gorgonio Constriction and the Boues Sea Embayment between California and Arizona. This served to isolate the Peninsular Desert from the Mojave and Sonoran deserts at

about 3 Mya. Then, two transpeninsular seaways divided the peninsula itself. The Cape Region was isolated at the Isthmus of La Paz around 0.3 Mya (Grismer, 1994), and a hypothesized Inner Peninsular Seaway may have isolated the peninsula about 1 Mya (Upton and Murphy, 1997). Lindell *et al.* (2006), however, proposed that these dates were likely older than first thought based on mtDNA studies of the herpetofauna. For instance, geological and paleontological data supports a date for the Inner Peninsular Seaway event from the late Miocene (11.6-5.3 Mya) to the early Pliocene (5.3-3.6 Mya).

For the split between the east and west Sonoran Desert indicative of the Boues Sea Embayment, our dates range between 5.79 and 2.98 Mya with an average of 4.33 Mya and older than those based on herpetofauna and mice (Riddle *et al.* 2000). Specific dates include 4.22 Mya (within the species *B. triangularis*) from *Brachycistis,* 2.98 Mya (*C. nubeculus* and its sister clade) for *Chyphotes*, and 5.79 Mya (*O. clypeata* and *O.* sp. nov. 9) for *Odontophotopsis.*

For the split between the Sonoran Desert in the northern half of the Baja peninsula and southern peninsular desert indicative of a hypothetical inner peninsular seaway, my dates range between 7.3 Mya and 1.33 Mya with the average being 3.47 Mya. Specific dates include 5.2 Mya (*B.* **sp. nov.** and *B. alcanor* + *B. vigilax*) from *Brachycistis,* 2.59 Mya (*C.* **sp. nov.** from Baja and its sister clade), and 1.33 Mya (*C.* **sp. nov.** and its sister clade) for *Chyphotes,* and 7.3 Mya (*O. dentifera* and its sister clade), 2.89 Mya (*O.* **sp. nov.** 4 and *O.* **sp. nov.** 5), 2.81 Mya (*O. serca* and *O.* **sp. nov.** 1), and 2.18 Mya (O. **sp. nov.** 6 and O. **sp. nov.** 7) for *Odontophotopsis*. The analyses of these wasps seem to indicate the existence of an inner peninsular seaway, but the dates are older than those

initially proposed. The analysis of *Odontophotopsis,* however, is missing the Sonoran species *O. denticoxa*, which is the putative sister species to *O. dentifera* based on a unique set of morphological characters the species share. Addition of this species in future analyses would likely bring the oldest date cited here closer to the other velvet ant dates with a range likely between 5.2 Mya and 1.33 Mya, which is in the range of the older proposed dates of late Miocene to early Pliocene .

5. Summary and Conclusions

Our analyses, which not only use traditional molecular data, but also utilize novel methods to analyze genomic data, clearly show that the high biodiversity found in North American deserts can be attributed to both Neogene orogenic events and Pleistocene climate change. Furthermore, our findings clarify some of the proposed geographic vicariant events that have been used to explain diversification in numerous plant and animal taxa. Future papers will address some of the taxonomic issues uncovered through our analyses, particularly in *Brachycistis*.

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CHAPTER 6

SUMMARY AND CONCLUSIONS

Summary

Nocturnal wasps are highly diverse throughout the southwestern Nearctic region. These species are ecologically important as parasitoids in aridlands due to the immense abundance. Previous molecular studies have made mutillids model organisms for biogeographical studies, such as Pitts et al. (2010) and Wilson and Pitts (2010, 2011). The goal of this dissertation was to continue to add to our knowledge of mutillids in arid systems, as well as investigate the utility of other nocturnal wasps, namely Brachycistidinae (Tiphiidae) and Chyphotidae, for further adding to our knowledge base. This dissertation first addresses a taxonomic issue in *Chyphotes* and then addresses the biogeography of nocturnal wasp species in the Mojave and Sonoran deserts.

This dissertation shows the value of the relatively new methods of phylogenomics for determining phylogenetic relationships over the old style of Sanger sequencing. At the beginning of this dissertation I was using single gene sequencing with poor results. For Mutillidae and Chyphotidae the majority of genes targeted worked, although not for every specimen. In contrast, *Brachycistis* was nearly impossible to get positive PCR results, required a significant amount of troubleshooting, and if amplification was successful sequencing often revealed pseudogenes. Fortunately, I was able to learn a new molecular technique during my dissertation. Ultra-conserved elements opened new doors to research with these groups. This method allowed the use of suboptimal specimens

(those that have been curated for a number of years, or samples that have degraded DNA) which meant rare species could be sampled for the first time. It also meant that groups previously impossible to amplify for single genes (*Brachycistis*) could be obtained with minimal effort. The hours spent in the lab trying to troubleshoot faint bands became a thing of the past. This method not only worked better, but reduced cost both to project finances and personal time commitment. It took me at least one year to get three genes to amplify well enough to produce a phylogenetic tree, now it takes me one month to gather datasets as large as 1,000,000 base pairs for 100 specimens. I plan to continue using this method to further explore biogeographical hypotheses for these groups.

Considering the success of using UCE loci for this dissertation, this offers a beginning point for future work on nocturnal wasps. One topic that was not completed during this dissertation, but is now very possible, is using this new method to help resolve further taxonomic issues. In Chyphotidae there are a number of subspecies that can finally be sunk with molecular data, and in both Chyphotidae and *Brachycistis* the taxonomy is based mostly on male only species. New molecular data would allow for sex associations that would further resolve these relationships. Beyond taxonomic issues, this new approach would be very successful at determining phylogeographic relationships. The original design of this thesis included examination of widespread species to look for phylogeographic patterns. Considering the difficulty in capturing single genes, this project never materialized, but is now possible.

References Cited

Pitts, J.P., Wilson, J.S., von Dohlen, C.D., 2010. Evolution of the nocturnal Nearctic Sphaeropthalminae velvet ants (Hymenoptera: Mutillidae) driven by Neogene orogeny and Pleistocene glaciation. Mol. Phylo. Evol. 56, 134-145.

Wilson, J.S., and J.P. Pitts. 2010. Illuminating the lack of consensus among descriptions of earth history data in the North American deserts: A resource for biologists. Progress in Physical Geography. 34: 419-441.

Wilson, J.S. and J.P. Pitts. (2011) Pleistocene connection between the Nearctic Mediterranean and desert regions in the *Spaheropthalma unicolor* species-complex (Hymenoptera: Mutillidae). Insect Conservation and Diversity. doi: 10.1111/j.1752-4598.2010.00124.x

APPENDICES

Appendix A

Coauthor Permission Letter

4 August 2017

Emily Sadler has my permission to include the following papers, which was submitted for publication, of which I was a co-author, in her doctoral dissertation.

Sadler, E.A., J.P. Pitts, and J.S. Wilson. "Nocturnal Velvet Ants (Hymenoptera: Mutillidae) of Joshua Tree National Park, Riverside County, California with the description of three new species."

Sadler, E.A., J.P. Pitts, and J.S. Wilson. "Faunal Study of the Nocturnal Aculeate Wasps (Hymenoptera) of the Sonoran and Mojave Deserts of Joshua Tree National Park."

Sadler, E.A., J.P. Pitts, and J.S. Wilson. "Reassessing species boundaries in the black-headed species of the subgenus *Chyphotes* Blake (Hymenoptera: Chyphotidae)."

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James P. Pitts

Appendix B

Copyright Letter

MAGNOLIA PRESS

Assignment of copyright

Name of Journal: *Zootaxa*

Title of the Article:
Naturnal velvetants (Hymenoptera: Mutillidae) of Joshua Tree National Park, Riverside County, California with a description of three new species

Corresponding Author
Emily Sadler sadler.e@gmail.com

Submission of this Article to *ZOOTAXA* implies that

1) All authors agree to its submission and the Corresponding author has been authorized by co-authors

2) This Article has not been published before and is not being considered for publication elsewhere

3) This Article does not violate any copyright or other personal proprietary right of any person or entity and it contains no abusive, defamatory, obscene or fraudulent statements, nor any other statements that are unlawful in any way

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Authorisation (if required) _____ Date _____

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CURRICULUM VITAE

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Phone (970)988-0355 • E-mail sadler.e@gmail.com

PERSONAL DETAILS

I have spent the past six years conducting research and working in the Entomology Museum of Utah State (EMUS) expanding the collection of nocturnal wasps, learning curatorial skills, and conducting tours. My research interests include studying the genetics and biogeography of the nocturnal wasp genus *Chyphotes,* as well as using genetic data to define sex associations. Along with single-gene sequencing I do phylogenomic sequencing using Ultra Conserved Elements (UCE). This research will lead to a better understanding of biogeographical distributions, speciation events in the deserts of North America, and ultimately a revision of the taxonomy and systematics of this genus. This research will also shed light on geographical events that shaped the flora and fauna of the North American deserts.

ACADEMIC QUALIFICATIONS:

Ph.D. **2011-present**
Biology
Thesis: *Historical Biogeography and Natural History of Nocturnal Wasps in the* S*outhwestern Deserts with Special Emphasis on the Genus* Chyphotes *(Hymenoptera: Chyphotidae)*
Utah State University

Bachelor of Science **May 2006**
Major: *Biological Science (concentration in Cellular, Molecular, and Genetic Biology)*
Major: *Zoology*
Minor: *Anthropology*
Colorado State University

PUBLICATIONS

Pitts, J.P. and **E. A. Sadler**. 2015. Description of a new species and species-group *Sphaeropthalma* Blake (Hymenoptera: Mutillidae) with an updated classification of the genus. *Zootaxa*. 3947: 282-288.

Sadler, E.A., J.P. Pitts, and J.S. Wilson. 2017. Nocturnal Velvet Ants (Hymenoptera: Mutillidae) of Joshua Tree National Park, Riverside County, California with the description of three new species. *Zootaxa* (accepted).

Sadler, E.A., J.P. Pitts, and J.S. Wilson. 2017. Faunal Study of the Nocturnal Aculeate Wasps (Hymenoptera) of the Sonoran and Mojave Deserts of Joshua Tree National Park. *Annals of the Entomological Society of America* (submitted).

Sadler, E.A., J.P. Pitts, and J.S. Wilson. 2017. Reassessing species boundaries in the black-headed species of the subgenus *Chyphotes* Blake (Hymenoptera: Chyphotidae). *Annals of the Entomological Society of America* (submitted).

Pitts, J.P. and **E.A. Sadler**. 2017. Association and description of the male of *Aplochares imitator* (Smith) (Hymenoptera: Pompilidae). *Zootaxa* (accepted).

Pitts, J.P., C. Waichert, and **E.A. Sadler**. 2017. Review of the Neotropical spider wasp genus *Anoplius* (*Dicranoplius*) Haupt (Hymenoptera: Pompilidae), new comb. *Zootaxa* (accepted).

Pitts, J.P. and **E.A. Sadler**. (In Preparation). Revision of *Odontophotopsis* Viereck (Hymenoptera: Mutillidae), Part 3, concerning the *O. melicausa* species-group.

E.A. Sadler, J.P. Pitts, M.G. Branstetter, and J.S. Wilson. (In Preparation). Comparative Historical Biogeography of the American Southwest with Emphasis on the Baja Peninsular Seaway Based on Three Groups of Nocturnal Wasps (Hymenoptera: Chyphotidae, Mutillidae, and Tiphiidae).

ACADEMIC AWARDS AND GRANTS

Utah State University Diversity Award- Student Category **2017**
Awarded to individuals who further the principles and values of affirmative action, equal opportunity, and diversity

Claude E. Zobell Scholarship ($1,000) **2016**
Awarded to outstanding graduate students within the College of Science in the fields of Biology, Chemistry & Biochemistry, Geology, and Physics.

Matt Del Grosso Award ($1,000) **2016**
Awarded annually by the Graduate Programs Committee in the Department of Biology at Utah State University. The award funds field research expenses for graduate students in the Department of Biology.

Utah State University Graduate Enhancement Award ($4,000) **2015**
Awarded to graduate students, based on merit, who have consistently shown a track record of excellence.

The Center for Women and Gender Travel Award ($200) **2014**
Awarded matching funds from The Center for Women & Gender. The center is dedicated to helping students at Utah State University succeed in their schooling and the award was used for travel to a national conference where I gave a presentation on my research.

Utah State University Research and Project Award ($1,000) **2014**
Awarded to graduate students actively pursuing their graduate degree to help with the necessary research or purchasing the necessary materials to complete their degree.

Utah State University Dissertation Enhancement ($12,000) **2013**
Award is a competitive funding opportunity for Ph.D. students to obtain a significant amount of money to augment their dissertation research, increase the quality of their dissertation, and lead to more publications for the student.

Utah State University Research and Project Award ($1,000) **2013**
Awarded to graduate students actively pursuing their graduate degree to help with the necessary research or purchasing the necessary materials to complete their degree.

Robert Lee Graduate Student Research Grant ($3,775) **2012**
Awarded to students in support of independent remote field research at Joshua Tree National Park and to provide the recipients with an opportunity to integrate their scientific research with land management issues.

Emory Slosson Scholarship ($1,000) **2001**
Awarded to students in their first year of undergrad with high academic promise.

RESEARCH ACTIVITY AND PRESENTATIONS

POSTER PRESENTATIONS

2015. **Emily Sadler** and James P. Pitts. "The good, the brown, and the ugly: comparative historical biogeography of nocturnal wasps (Hymenoptera: Chyphotidae, Mutillidae, Tiphiidae)," poster presented at the 63rd Annual Meeting of the Entomological Society of America, Minneapolis, Minnesota.

2014. Rebecca Condie, **Emily A. Sadler** and James P. Pitts. "Systematics & Phylogenetics of Pseudomethocini (Hymenoptera: Mutillidae)," poster presented at the Utah State University Department of Biology Spring 2014 Undergraduate Research Symposium.

2014. **Emily A. Sadler** and James P. Pitts. "A Tale of Two Subfamilies: Chyphotinae and Typhoctinae (Hymenoptera: Chyphotidae)," poster presented at the 98th Annual Meeting of the Pacific Branch of the Entomological Society of America, Tucson, Arizona. ***Awarded 1st place.***

2013. **Emily A. Sadler** and James P. Pitts. "Shedding Light on Nocturnal Insect Evolution in the Pleistocene," poster presented at the 2013 Evolution Conference, Snowbird, Utah.

2013. Lauren M. Peless, **Emily A. Sadler** and James P. Pitts. "Was Evans Evidently Correct about *Evagetes* (Hymenoptera: Pompilidae)?" poster presented at the Utah State University Department of Biology Spring 2013 Undergraduate Research Symposium

2011. **Emily Sadler** and James P. Pitts. "The Black-headed Conundrum: Species boundaries in *Chyphotes* (Hymenoptera: Chyphotidae)," poster presented at the 96th Annual Meeting of the Pacific Branch of the Entomological Society of America, Portland, Oregon. ***Awarded 2nd place.***

2007. E. Apple Snider, Kenneth R. Wilson, Crystal L. Cooke, and **Emily A. Sadler**. "Insect communities in burned and unburned piñon-juniper woodlands of Mesa Verde National Park, Colorado," poster presented at the Association for Fire Ecology Conference.

ORAL PRESENTATIONS

2016. Emily A. Sadler, James P. Pitts, and Joseph S. Wilson. "A wasp's tale: understanding the present by revealing the past (Hymenoptera: Chyphotidae, Mutillidae, and Tiphiidae)" Late Breaking Symposium "Making Species Inventories Work For You: Diverse Uses Across Varied Fields" at the 25th International Congress of Entomology meeting, Orlando, Florida. ***Invited speaker*** and ***symposium co-organizer***.

2016. **Emily Sadler**, Katie Weglarz, Dave Denlinger, and Corey Andrikopoulus. "Broadening Navajo Perspectives: Lessons Learned by the Ch'osh Tribe." Diversity Symposium at the 100th Annual meeting of the Pacific Branch of the Entomological Society of American, Honolulu, Hawai'i. ***Invited speaker*** and ***symposium co-organizer***.

2015. **Emily A. Sadler** and James P. Pitts. "Comparative Historical Biogeography of the Southwest Using Three Families of Nocturnal Wasps" Symposium at the 99th Annual meeting of the Pacific Branch of the Entomological Society of American, Coeur d'Alene, Idaho. ***Invited speaker***

2015. James P. Pitts**, Emily A. Sadler** and Joseph S.Wilson. "Historical Biogeography of the Southwestern USA: A Lack of Consensus" Symposium at the 99th Annual meeting of the Pacific Branch of the Entomological Society of American, Coeur d'Alene, Idaho.

2014. **Emily A. Sadler** and James P. Pitts. "Historical Biogeography of the Enigmatic Chyphotid Wasps (Hymenoptera: Chyphotidae)," The 62nd Annual Meeting of the Entomological Society of America, Portland, Oregon. ***Awarded 1st place.***

2013. **Emily Sadler** and James P. Pitts. "The Good, the Brown, and the Ugly: Biogeography of Little Brown Wasps (Hymenoptera: Chyphotidae)," The 61st Annual Meeting of the Entomological Society of America, Austin, Texas.

2013. **Emily Sadler** and James P. Pitts. "A Million Little Brown Wasps (Chyphotidae, Mutillidae, and Tiphiidae: Hymenoptera): A Survey of Joshua Tree National Park," Symposium at the 61st Annual Meeting of the Entomological Society of America, Austin, Texas. ***Invited speaker***

2012. **Emily Sadler** and James P. Pitts. "The Black-headed Conundrum: Species boundaries in *Chyphotes* (Hymenoptera: Chyphotidae)," The 60th Annual Meeting of the Entomological Society of America, Knoxville, Tennessee.

2012. **Emily Sadler** and James P. Pitts. "Systematics of the "Well-Known" Family Chyphotidae (Hymenoptera)," The 60th Annual Meeting of the Entomological Society of America, International Society of Hymenopterists Symposium, Knoxville, Tennessee.

2011. **Emily Sadler** and James P. Pitts. "The Black-headed Conundrum: Species boundaries in *Chyphotes* (Hymenoptera: Chyphotidae)," Intermountain Graduate Symposium, Logan, Utah.

GUEST LECTURES

2015. **Emily Sadler**. "Nocturnal wasps…mostly." Lecture on natural history and how to identify nocturnal wasps of the U.S. for BIOL 4750/6750 Hymenoptera Course.

2015. **Emily Sadler**, Michael Orr, and David Denlinger. "Biodiversity: Insects and Arachnids!" Gave lecture and did demonstrations with insects and arachnids for BIOL 1010 Science and the Citizen.

2015. **Emily Sadler**. Chapter 19: Gene function and therapy. Gave lecture for BIOL 3060 Genetics.

2015. **Emily Sadler**. Chapter 19: Molecular Cloning & PCR. Gave lecture for BIOL 3060 Genetics.

OUTREACH

ORAL PRESENTATIONS

2016. Katie Weglarz and **Emily Sadler**. "Native American Mentorship STEM Summer Program." Presented at the Broader Impacts Faculty Workshop at Utah State University.

2016. **Emily Sadler**. "Small Wonders: The expansive and colorful work of insects." An opening talk at the USU Entomology Club and USU Merrill-Cazier Library collaborative educational library exhibit.

2015. Michael Orr and **Emily Sadler**. "How to make a good scientific poster." Utah State UG Research Symposium Poster Help Session.

2015. Jonathan B. Koch and **Emily A. Sadler.** "Is this real?: Promoting insect science in northern Utah" presented at a symposium at the 99th Annual meeting of the Pacific Branch of the Entomological Society of American, Coeur d'Alene, Idaho.

2014. Emily Sadler. "A wasp by any other name" presented at a USU Entomology Club Valentine's Day Movie night. Introductory talk on wasps and female entomologists before screening the classic 1959 movie The Wasp Woman.

CLUBS & EVENTS AT USU

USU Society for the Advancement of Chicanos/Hispanics and Native Americans in Science (Secretary 2013-2014, Vice President 2014-2015, Vice President 2015-2016)

Participated in events to interact with the community like A-days, Day on the Quad, and the USU Annual Pow-wow where we answered questions about the SACNAS chapter and encouraged people to join. I designed flyers for events, and made caramels for a holiday candy sale to raise funds for the club.

Academic Committee Representative (Biology Department 2015-2016)

Current student representative for Biology Department; participated in the review of a new graduate course at USU on communicating science.

USU Entomology Club (Vice President 2013-2014, President 2014-2015)

Designed club logo and club shirts for sales, led outreach events for Valentine's Day and Halloween to educate the public about insects. Volunteered at five Science Unwrapped Lectures and designed eight educational posters about insect related topics. Helped design club website and continue to maintain it. Helped create an educational display done in collaboration with the Merrill-Cazier library. I also wrote text for the display, was one of three graduate students that helped in editing the text, design, and layout, and I gave an introductory talk on mimicry and current research at USU at the opening.

USU Insect Tours (2013-2015)

Personally led five tours of the insect teaching collection for visiting classes (K-12 and College Freshman), assisted with two tours led by other graduate students reaching 175 students and educating them on the importance of insects.

USU Allies on Campus (2014)

Completed Ally training and continue to support the LGBTQ community and am committed to providing a "safe zone" in both my teaching and work spaces.

EVENTS IN THE COMMUNITY

2015. Heritage Elementary Science Fair Insect Demonstrations

Heritage Elementary School, Nibley, UT.

Science demonstrations to inspire students for their science fair project. I had termites on display to show chemical trails, mosquitoes of all stages to teach about their lifecycles, and pinned insects to demonstrate insect mimicry.

2013. Science Fair Judge
Hillcrest Elementary, Logan, UT.
Served as a judge of the (K-5) student's science fair projects. Spoke with students on their projects, graded and gave feedback on their posters, and handed out awards.

2013. Graduate Student Panel
Utah State University, Logan, UT.
Sat on a panel for Dr. Sullivan's Women in Science class to answer questions and discuss our experiences as graduate students, and our experiences as undergraduates transitioning to graduate school life.

NEWS COVERAGE OF OUTREACH

Opsahl, Kevin. "USU Eastern students conclude Native American Mentorship Program." 06 Jun 2017. http://news.hjnews.com/allaccess/usu-eastern-students-conclude-native-american-mentorship-program/article_60d90a28-286e-5d91-8303-c1182da95478.html

Opsahl, Kevin. "USU club seeks to open eyes of public to world of insects." *The Herald Journal*. 08 Feb 2016. <http://news.hjnews.com/allaccess/usu-club-seeks-to-open-eyes-of-public-to-world/article_8c1ae804-d60c-5619-ad42-318fa1a91d36.html>

Milovich, Rose. "Feeling Bugged? See the New Exhibit at USU's Merrill-Cazier Library." Utah State University, Utah State Today. 4 Feb 2016. <https://www.usu.edu/today/?id=55490>

DeVilbiss, John. "Confidence Building at its STEM: Blanding Students Gain Confidence in STEM Fields." Utah State University Eastern Blanding Campus, News. 2 Dec 2015. <https://sjc.usu.edu/htm/news/articleid=30389>

EXPERIENCE

Adjunct Instructor for Biology 2988

May-June 2017
Utah State University Eastern Blanding Campus
Department of Biology, Blanding, UT

Course Description: Students kept journals and submitted reflective writing assignments allowing us to assess changes in attitudes and scientific knowledge over the month they were in the course. The course included each student making a poster explaining their experiences and what they gained from the month long mentorship program.

Native American Mentorship Program Co-Lead Graduate Facilitator

February-June 2017
Utah State University
Department of Biology, Logan, UT

Description: Supervise 20 visiting USU Eastern Blanding students during summer work on Logan campus.
Duties: Recruit and organize labs for students to work in during the summer, schedule social activities, serve as point of contact for labs participating in the program, and serve as a primary contact with students.

Graduate Prep & Teaching Assistant Biology 1625 (Honors)

January-May 2017
Utah State University
Department of Biology, Logan, UT

Description: Preparing materials for all introductory Biology Labs (1625) and teaching assistant for the same class.

Duties: Preparing lab setup and maintenance of class materials for 24 sections. Teaching new topics each week, grading assignments. I was responsible for teaching 1 section, the Honors Students section.

Adjunct Instructor for Biology 2988

May-June 2016
Utah State University Eastern Blanding Campus
Department of Biology, Blanding, UT

Course Description: Students kept journals and submitted reflective writing assignments allowing us to assess changes in attitudes and scientific knowledge over the month they were in the course. The course included each student making a poster explaining their experiences and what they gained from the month long mentorship program.

Native American Mentorship Program Co-Lead Graduate Facilitator

February-June 2016
Utah State University
Department of Biology, Logan, UT

Description: Supervise 25 visiting USU Eastern Blanding students during summer work on Logan campus.

Duties: Recruit and organize labs for students to work in during the summer, schedule social activities, serve as point of contact for labs participating in the program, and serve as a primary contact with students.

Graduate Teaching Assistant Biology 1010

August-December 2016
Utah State University
Department of Biology, Logan, UT

Description: Introductory biology class for non- majors.

Duties: Grading assignments throughout the semester for 246 students.

Graduate Research Assistant

2015-2016
Utah State University
Department of Biology, Logan, UT

Description: Working on gathering data for thesis, submitting publications, and helping in the Entomological Museum of Utah State University.

Native American Mentorship Program Co-Lead Graduate Facilitator

April-June 2015
Utah State University
Department of Biology, Logan, UT

Description: Supervise 21 visiting USU Eastern Blanding students during summer work on Logan campus.

Duties: Recruit and organize labs for students to work in during the summer, schedule social activities, serve as point of contact for labs participating in the program, and serve as a primary contact with students.

Native American Mentorship Program Graduate Facilitator

May-June 2014
Utah State University
Department of Biology, Logan, UT

Description: Supervise four visiting USU Eastern Blanding students during summer work on Logan campus.

Duties: Organize social activities, coordinate with labs participating in the program, and serve as a primary contact with students.

Graduate Prep Teaching Assistant Biology 1610/1620

2012-2015
Utah State University
Department of Biology, Logan, UT

Description: Preparing materials for all introductory Biology Labs (1610/1620).

Duties: Preparing lab setup and maintenance of class materials for 20-32 sections. Occasionally lead lab meetings and supervise other GTA's.

Graduate Teaching Assistant Biology 1610/1620

2011-2014
Utah State University
Department of Biology, Logan, UT

Description: Teaching assistant for introductory Biology Laboratory classes (1610/1620).

Duties: Taught new topics each week, graded assignments and prepared lab setup occasionally. Responsible for two to three sections each with 30 students.

Lab Coordinator

2007-2011
AECOM Fort Collins Environmental Toxicology Lab
Fort Collins, CO

Description: Coordinated projects and staff in the day-to-day operations at a commercial water toxicology laboratory.

Duties: Set up and maintained WET (Whole Effluent Toxicity) experiments as well as care for the culture organisms used in them. Testing required the use and maintenance of micropipetters, refractometers, photometers, hemacytometers, pH meters, dissolved oxygen meters, conductivity meters, mass spectrometers, total residual chloride (TRC) meter, ammonia meter, dilutor panels, and the proper use of muffle furnaces to assess ash free dry weights. Other responsibilities included overseeing scheduling of lab staff and lab projects, interviewing and hiring new staff, training newly hired staff, and continually monitoring their progress. Led laboratory meetings, maintained a line of communication between supervisors and technicians, and lead technician on specialty projects.

Lab Technician

2007
Colorado State University
Department of Fish, Wildlife, and Conservation Biology, Fort Collins, CO

Description: Assisted researcher, Apple Snider, with ongoing research projects collecting insect species at Mesa Verde National Park, CO.

Duties: Collected and identified insects down to the Family level to develop a census of local insect populations. Used those data to determine

the feeding ecology of native bat populations and to better determine what steps are needed for their conservation.

Student Worker

2005-2006
Colorado State University
Department of Fish, Wildlife, and Conservation Biology, Fort Collins, CO

Description: Assisted in two research experiments dealing with the effects beetles had on invasive plant species.

Duties: Weighing and dissecting plants to retrieve beetles as well as documenting root biomass in potted plants.

Contractor

2002-2005
Visible Productions
Fort Collins, CO

Description: Created computerized (digital), anatomically correct, 3D models from Computer Tomography (CT) and Magnetic Resonance Image (MRI) data for use in interactive multimedia, educational programs.

Duties: Generated models, cleaned models and readied them for use in other programs.

PROFESSIONAL AFFILIATIONS AND MEMBERSHIPS

SEMINARS & WORKSHOPS

Scientific Programming Bootcamp **March 23-24, 2013**
Utah State University, Logan, UT

Graduate Student Writing Seminar **February 27, 2013**
Utah State University, Logan, UT

Workshop in Molecular Evolution **January 21, 2013-February 3, 2013**
Cesky Krumlov, Czech Republic

Hymenoptera Course **August 5-12, 2012**
Tovetorp Zoological Research Station, Sweden

MEMBERSHIPS

Entomological Society of America (Pacific Branch; SysEB)
International Society for Hymenopterists
Society for Systematic Biologists